CHAPTER 7

DWARF-SHRUB HEATHS

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In literature, legend and in the affections of the people, heath vegetation has a central place among the characteristic features of Scottish landscape, and heather (*Calluna vulgaris*), the most widespread dominant, has acquired the status of a national flower. The communities of which the heathlands are composed occupy extensive areas, being in some cases particularly fine examples of their kind (Plates 37 and 38), and form part of a series which extends throughout much of Britain and the neighbouring oceanic and sub-oceanic parts of W. Europe, from S.W. Norway to Spain. While in many parts of this area heathlands are now rapidly being replaced by plantations and farm land, in Scotland heath is still retained and regarded by many as a vegetation-type which is not only attractive but valuable. Its value lies in the provision of grazing throughout the year in climates and on soils and terrain where to substitute a richer herbage would at present be uneconomic. Considerable stocks of sheep, and in some districts cattle also, are supported, while extensive areas are managed as grouse-moor or "deer forest" for sporting purposes: in numerous instances the requirements of sheep and grouse are combined. In the past the extent of heathland has been even greater, occupying much of the Lowlands now claimed by agriculture, industry and urban development. Today, the heaths with which this chapter is concerned, those of the forest zone or land below the tree limit, reach their greatest extent in the foothills, glens and lower slopes of the upland regions of the country. They are represented also in coastal districts, but only in a fragmentary way in the intervening territory. Similar communities occur on drained, or drying, peat-bogs.

The W. European heath formation extends from low-arctic and montane climatic regimes to conditions approaching those of the Mediterranean. An oceanic type of climate, however, is essential for its development, which requires not only the absence of temperature extremes but also an abundant and well-distributed rainfall with maintenance of a generally high atmospheric humidity. Under these conditions, heaths will develop on acidic soils, generally of low fertility, wherever forest is excluded. The whole of Britain falls within their climatic range and in Scotland there are few districts lacking examples of some type of heath community, although in the lowlands they may be confined now to small areas unfit for agriculture. However, they are clearly more vigorous

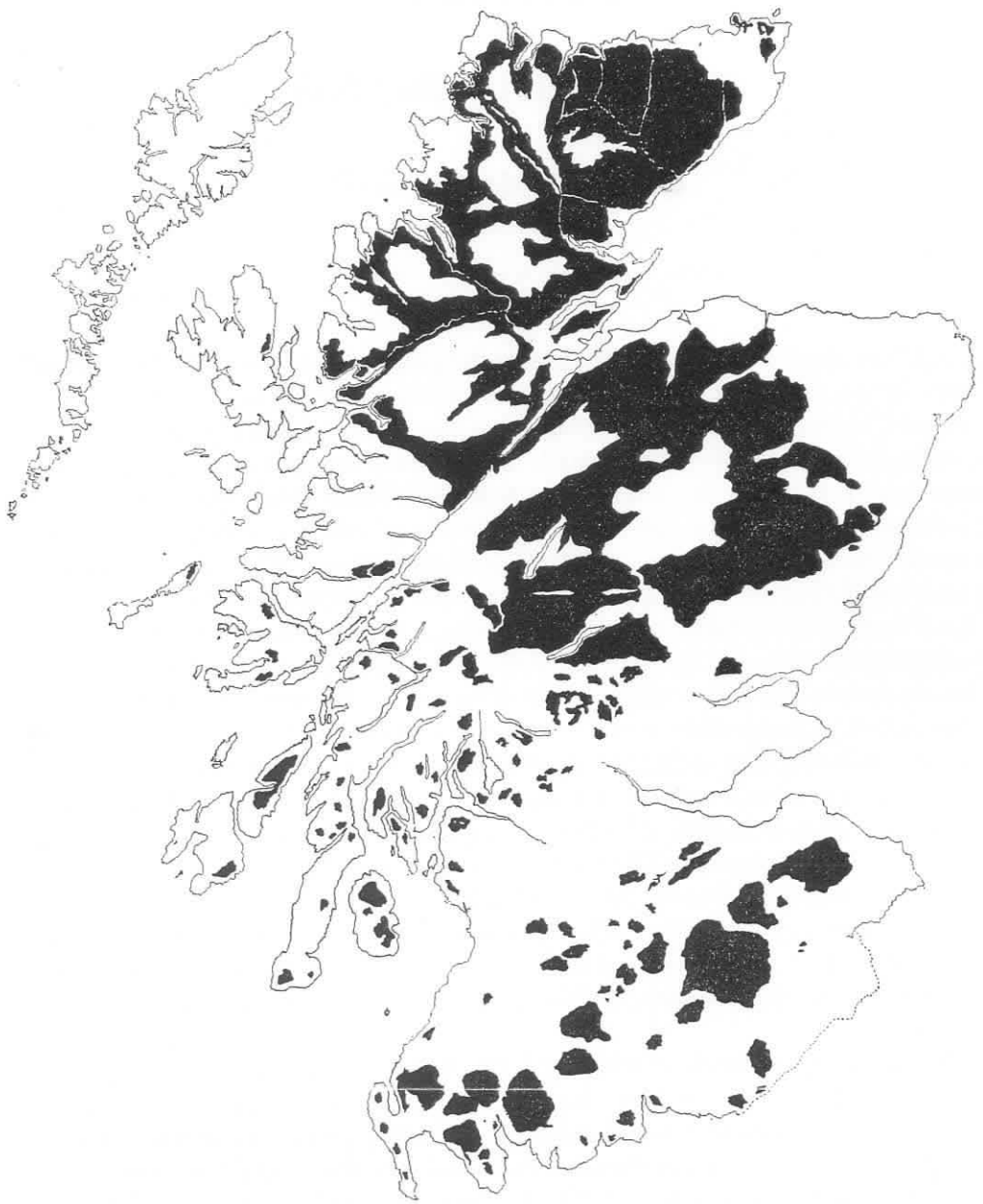


FIG. 38 Heath areas in Scotland. (Map compiled by C. L. Whittles (1950), *The Scottish Beekeeper*, **26**.) There is no map available showing the full extent of dwarf-shrub heaths in Scotland. However, the map reproduced here, restricted to areas in which *Calluna vulgaris* is extensively dominant, gives a useful impression of the general distribution of heathland.

in some districts than others and are perhaps best developed in the central and eastern upland regions where soils are generally acidic and of low base status, while rainfall lies between about 435 and 870 mm. (25-50 in.) per year (Fig. 38). On the more fertile soils, for example on many of the Perthshire hills, grassland often has a competitive advantage over heath, particularly under the added influence of grazing. Heath also largely gives place to other types of vegetation on the blanket peat of the hyper-oceanic western districts, where it becomes restricted to the steeper slopes or other very freely drained habitats.

The soil types on which heaths occur in Scotland include blown sand on fixed dunes (silicate syrosem), brown forest soils of low base status (oligotrophic braunerd), semi-podsols, podsols and drained peat. On the latter types a series of related communities may be traced from sites with free drainage ("dry" heath communities) to those with impeded drainage ("wet" heath communities), but where the substratum is waterlogged for much of the year and peat-building is active, heath is replaced by related bog communities (see Chapter 10).

The most usual soil profile to find below heath vegetation in Scotland is that of the iron humus podsol, with very variable development of the $\mathbf{A}_0$ (raw humus) horizon. Differences in depth of this horizon contribute to the general distinction made by gamekeepers and shepherds between "hard ground", on which the organic horizon is quite thin (up to about 5 cm.), and "soft ground" which incorporates podsolic soils with deeper organic horizons and peats. This distinction has proved of value in ecological investigations (Whittaker, 1960, 1961; Whittaker and Gimingham, 1962; see also Metcalfe, 1950). Beneath the purely organic layer there is frequently a horizon in which leached mineral grains are associated with humus ($\mathbf{A}_1$). Below this again a typical ash-grey $\mathbf{A}_2$ horizon may be visible, but in soils on which *Calluna* has long been dominant this may be masked by the presence of dark humic matter in some quantity throughout. A thin iron pan beneath the $\mathbf{A}_2$ is a common feature under *Calluna*-dominated vegetation, and where this pan is strongly developed it may impede drainage, leading to gleying of the $\mathbf{A}_2$ horizon and peat formation at the surface, with accompanying vegetational changes (cf. Plate 2 and p. 45).

Over most of its area heath has originated only after forest clearance, and its maintenance depends upon the continuance of practices which preclude a return of trees, normally periodic burning, or grazing by domestic animals, or a combination of both. In the absence of control by man, heath would in many cases give place to other vegetation, usually scrub or woodland, and consequently its status must be described as "semi-natural". It bears, however, a very close relationship to the climatic regime of W. Europe and, to this extent, can be regarded as a distinct regional formation occurring naturally where exposure, soil immaturity (as on fixed dunes) or occasionally soil infertility, limit the entry of trees. Indeed, on certain heathlands, once part of the native forest, trees will not nowadays readily recolonise, even where protected from burning and grazing, while commercial afforestation, although possible, is attended by certain difficulties. Such cases lead to unresolved debate on the status of heath vegetation, which on the one hand can be regarded as semi-natural if its origin was initially dependent on forest clearance,

or, on the other, as a natural development in harmony with the environment, the role of man being merely that of "triggering-off" or accelerating a more or less natural replacement of forest by heath.

Apart, however, from the poorest soils and most exposed situations, a cessation of control by burning or grazing normally soon results in an invasion by birch (*Betula* sp.), often with rowan (*Sorbus aucuparia*)—as occurred on parts of several moors (for example Dinnet, Aberdeenshire) during and shortly after the 1939-45 war when staff for managing large acreages was lacking (cf. p. 270). Birch, sometimes accompanied or followed by Scots pine (*Pinus sylvestris*), may before long establish a closed canopy. However, "muir-burn" (the regular firing of heathland) is employed not only to prevent tree regeneration but also to promote new, young growth of *Calluna* which provides an important proportion of the diet of sheep and cattle when grazed on the heath, and of the red grouse (*Lagopus scoticus*). The rotational burning of sections of the "moors", which in Scotland is carried out as far as possible in the early spring but also to a considerable extent in autumn, is thus a fundamental aspect of moorland management and an ecological factor having profound effects (cf. p. 272).

The first ecological descriptions of Scottish heaths were those by R. Smith (1900), W. G. Smith (1902, 1905, 1911) and Hardy (1904). It is surprising, particularly in view of the importance of heathlands in the economy of the more sparsely populated parts of the country, and of the tensions between the interests of sheep-farming, sport and forestry in their use and development, that until recently they received little further attention from ecologists. Tansley (1949) in *The British Islands and their Vegetation* could do no more than base a brief account of Scottish heaths on the section contributed by W. G. Smith to the "Types of British Vegetation" (1911). Since then, however, a number of papers bearing on aspects of the ecology of heaths in Scotland have begun to dispel ignorance of the history of these communities, the influences at work in them, and the potentialities for their development. Several organisations such as the Nature Conservancy, the Hill Farming Research Organisation and the Macaulay Institute for Soil Research as well as University Botanical Departments and the Colleges of Agriculture are actively promoting research in this sphere, and the following account owes much to recent work in several of these centres.

General Aspects of Community Structure and Physiognomy

Dominant species and life-forms

Scottish heathland vegetation is in the main dominated by heather (*Calluna vulgaris*), which sometimes forms virtually pure stands over extensive areas. Since this species is a community dominant throughout such a wide range of habitat conditions there is considerable floristic diversity in the communities established under its influence (pp. 253-267). The use of the term "Callunetum" so common in the literature, therefore conveys little ecological information in the absence of further qualification.

Other species of Ericaceae such as *Erica cinerea*, *E. tetralix*, *Vaccinium myrtillus*, *V. vitis-idaea*, *Empetrum nigrum* and *Arctostaphylos uva-ursi* are often associated with *Calluna*, and under appropriate conditions one or more of these may equal it in importance or replace it as dominant. The leading species are all much branched, woody dwarf-shrubs. *Calluna* is often 0·75 m. in height and may exceed 1 m. (Plates 39 and 40), *Vaccinium myrtillus* may sometimes equal it, while *Erica cinerea*, *Vaccinium vitis-idaea* and *Erica tetralix* are generally shorter. All these, however, under favourable conditions are nanophanerophytes (renewal buds between 25 cm. and 2 m. above soil surface), but may behave as chamaephytes (renewal buds up to 25 cm. above surface) in more severe habitats. In *Empetrum nigrum* and *Arctostaphylos uva-ursi* the chamaephyte life-form is the more usual.

Apart from the occurrence of isolated trees or tree seedlings, the only other life-form of importance among the flowering plants of heath communities is the hemicryptophyte, into which fall most of the important grasses and sedges, e.g. *Deschampsia flexuosa*, *Molinia caerulea*, *Nardus stricta*, *Trichophorum cespitosum*, *Eriophorum* spp., *Carex binervis*, *C. pilulifera*, etc.

Table 23 gives a series of biological spectra from a variety of heath communities in Scotland, showing that in terms of species the hemicryptophytes may often be in excess of the combined figures for nanophanerophytes and chamaephytes, but the latter always contribute the greater cover and mass of the vegetation. The same is true of the examples of Scandinavian heaths included for comparison.

Stratification

Where scattered trees or tree seedlings occur these may be regarded as pioneers or relics of forest communities rather than as integral components of heath vegetation. Occasionally, however, shrubs such as *Juniperus communis* and *Ulex europaeus* occur with some regularity or form patches in heath communities, but they are scarcely now as typical a feature of Scottish heaths as they are of some related Scandinavian or W. European ones. Since the stratum they represent is so discontinuous or localised it has little effect on conditions below it and is ignored in the following discussion.

A closed canopy is normally formed by *Calluna*, at least in stands exceeding 5-8 years of age, sometimes in association with other species. Its height depends upon the habitat and the age of the stand: it may either be very uniform in an even-aged stand, such as frequently results from regeneration after burning, or undulating in an uneven-aged stand. Whereas in the former the canopy is often uninterrupted over large areas, in the latter there may be frequent gaps where the centre of an old bush has died out. On hill slopes the vegetational profile may resemble a series of descending waves owing to the main frame-branches of all plants becoming decumbent and parallel in the downward direction, so that the canopy of each bush comes to overlap the basal parts of the next below it.

Calluna-dominated communities are generally more or less distinctly stratified and

TABLE 23

Representation of Life-forms in Selected Examples of Heath Communities

Locality	Community-type	Proportion of species in each Raunkiaer Life-form Group as % total number of Phanerophyte species				No. of Phanerophyte species	No. of Bryophyte species	No. of Lichen species
		N*	Ch	H	G			
Yesnaby, Orkney	Oceanic *Calluna—Erica cinerea*	14·3	28·6	57·1	...	14	8	2
Daviot, Inverness-shire	*Calluna—Vaccinium*	11·1	22·2	55·6	11·1	18	7	2
Strathfinella Hill, Kincardineshire	*Calluna—Vaccinium*	11·5	15·4	65·4	7·7	26	16	4
Dinnet, Aberdeenshire	*Calluna—Arctostaphylos*	9·1	22·7	68·2	...	22	10	5
Forvie, Aberdeenshire	*Calluna—Empetrum nigrum*	...	16·7	83·3	...	12	7	11
Karmøy, S.W. Norway	Oceanic *Calluna—Erica cinerea*	14·3	10·7	67·9	7·1	28	11	4
Hallandsåsen, S.W. Sweden	*Calluna—Vaccinium*	17·6	11·8	58·8	11·8	17	11	3
Nörrevosborg, W. Jutland, Denmark	*Calluna—Empetrum nigrum*	16·7	33·3		16·7	6	6	12

N* = Nanophanerophytes H = Hemicryptophytes

Ch = Chamaephytes G = Geophytes

Based on flora lists from areas of 40 sq. m.

this stratification is associated with the development of characteristic micro-climatic regimes which are of importance in the regeneration of *Calluna* itself and other species of the community, and in the establishment of tree seedlings. In well-developed heath communities, common in the moist upland regions, four strata may be differentiated. (Simpler versions which appear in other habitats are described later, p. 239.)

Heaths with dense canopy and four strata. The most complex type of stratification frequently takes a form such as the following:

(i) *Calluna* canopy at its densest between 25 cm. and 40 cm. above ground, scattered branches extending to between 60 and 80 cm. or more.
(ii) Second stratum, discontinuous, at about 10-20 cm., consisting of subordinate dwarf-shrubs (e.g. *Vaccinium* spp., *Empetrum nigrum*) and grasses or sedges (e.g. *Deschampsia flexuosa*, *Carex binervis*, *Eriophorum* spp. or *Trichophorum cespitosum*).
(iii) Third stratum, at about 5-10 cm., of robust mosses, e.g. *Pleurozium schreberi*, *Hylocomium splendens* and low-growing herbs, e.g. *Potentilla erecta*, *Galium saxatile*.
(iv) Fourth stratum, the "ground stratum", of mat-forming or short erect mosses, e.g. *Hypnum cupressiforme*, *Pohlia nutans* and lichens.

Micro-climatic conditions. These strata exert marked effects upon micro-climatic conditions. Light intensity is reduced by the *Calluna* canopy to less than 20 per cent. of that in the open, while at ground level under the additional strata it may fall to below 0·5 per cent. This factor alone plays a large part in controlling the establishment of plants beneath the canopy and restricts the regeneration of *Calluna* itself to gaps in the canopy, since individuals will not normally survive long under less than 40 per cent. daylight.

The close-packed arrangement of shoots at the periphery of the bush is effective in retarding air-movement. For example, when a wind speed of 2·6 m./sec. (8½ ft./sec.) was recorded at 1 m. above ground on a heath near Aberdeen, the speed at canopy-level was only about 0·8 m./sec. (2½ ft./sec.). At ground level below dense moss strata air-flow is normally eliminated except perhaps when gales are blowing above, since as Geiger (1959) points out, "the retarding effect of a low plant cover is relatively less, the higher the wind velocity". The above measurements closely parallel those given by Stocker (1923) for a heath near Bremerhaven.

Temperature and humidity conditions also relate very closely to stratification, but although several investigators (e.g. Delany, 1953; Stoutjesdijk, 1959) have measured temperature profiles on passing from the air above heath vegetation down through the canopy to the ground, comprehensive data on this are lacking. Table 24 (p. 240) gives some representative measurements from Scottish heaths. In cloudy weather there is little difference between the temperature of the air surrounding the *Calluna* shoots at canopy level and that at a height of 1 m. above ground. In still, sunny weather, however, the

temperature at canopy level may be several degrees higher. This may produce a local drop in relative humidity and consequently promote evaporation from the plants. In windy weather, by contrast, there is rather more mixing of the air; temperature and humidity differences are then lessened, although the marked reduction of air movement at canopy level already noticed will tend to maintain them to some extent.

Rather little solar radiation penetrates the canopy in this type of community, so that temperature usually remains lower and more constant within, while humidity is higher. The moss strata generally remain moist except in drought periods, and at ground level an even more constant environment is maintained, slow to warm up and yet well protected from intense cold. In summer the ground temperature is usually between 2° and 5° lower than that of the canopy, while relative humidity is normally about 80 per cent., frequently remaining for long periods about 95 per cent. As Leyton (1955) and others have pointed out, *Calluna* vegetation of this kind is effective in conserving surface moisture. This is an important factor affecting community composition and may also have some influence on the establishment of planted tree seedlings.

In winter, reduction in temperature by radiation away from the plants on clear, cold nights will reverse the pattern described above, being greatest in the upper part of the canopy. This may lead in frosty weather to thick deposits of rime on the shoots. Where, as so often, the surface of the canopy is undulating, the slight hollows may be shaded from the low winter sun throughout much of the day and the rime will then remain clothing the shoots. In warmer weather, these shaded patches may remain saturated with moisture as the rest drys out during the day.

Simpler types of community structure. In habitats less favourable for the development of the complex type of community structure one or more of the main strata may be lacking, while those represented may be less dense, or interrupted by gaps. A very common type is that in which the canopy produced by a luxuriant even-aged stand of *Calluna*, resulting from well-controlled burning management, becomes so dense as to exclude all other strata with the exception of a sparse ground stratum of mosses or lichens developed in patches beneath the thinner parts of the canopy. Elsewhere the ground is covered in a thick deposit of *Calluna* litter.

The drier substrata often lead to a lower and more patchy *Calluna* canopy, usually at about 20-30 cm., with an irregular second stratum of subordinate dwarf-shrubs such as *Erica cinerea* at about 15 cm., and a more or less well-developed ground stratum of mosses and lichens. In very exposed situations this type of structure may be reduced still further to two strata only, with a low, even, but not dense, *Calluna* canopy at about 10-15 cm. and a discontinuous ground stratum consisting predominantly of lichens. In both cases much bare ground is visible from above and a micro-climatic regime considerably different from that described in the previous section is operative. Light intensity at ground level is often as high as 60 per cent. of that above the vegetation, and where the *Calluna* canopy is low and rather open it seldom falls below 20 per cent. Correspondingly, more radiation reaches the lower levels, and maximum temperatures in sunny weather may be recorded at ground level rather than in the canopy (Delany, 1953).

TABLE 24

Examples of Temperature and Humidity Profiles in *Calluna* Communities

Height above ground at which determinations were made (cm.)	Series 1 Sun after frost T (°C.)	Series 1 Sun after frost R.H. (%)	Series 2 Sun after frost T (°C.)	Series 2 Sun after frost R.H. (%)	Series 1 Heavy cloud T (°C.)	Series 1 Heavy cloud R.H. (%)	Series 2 After 1 hr. full sun, following heavy cloud T (°C.)	Series 2 After 1 hr. full sun, following heavy cloud R.H. (%)	Series 1 Hazy sun, no wind T (°C.)	Series 1 Hazy sun, no wind R.H. (%)	Series 2 Full sun, light wind T (°C.)	Series 2 Full sun, light wind R.H. (%)	Series 1 Windy, with drizzle T (°C.)	Series 1 Windy, with drizzle R.H. (%)	Series 2 Clearing after rain T (°C.)	Series 2 Clearing after rain R.H. (%)	Series 3 Sun after rain T (°C.)	Series 3 Sun after rain R.H. (%)	Series 4 Full sun, moderate wind T (°C.)	Series 4 Full sun, moderate wind R.H. (%)
100	5·7	70·0	6·8	66·0																
90																				
80																				
70																				
60																				
50	5·8	69·5	7·5	67·5																
40			8·6	62·5	3·3	93	4·4	94·5	14·8	62·0	14·4	56·5					14·2	72		
30			7·6*	70·0*									11·2	90	13·2	71	15·2	73	16·5	61
20	6·8	67·5			3·2	88	4·4	90·5	14·4	65·5	14·2	63·5	11·1	93	13·3	78			16·1	62
10	5·0*	96·5*	5·4*	94·0*																
Ground level	5·0*	94·5*	5·2*	96·5*	3·2*	88*	3·7*	95·5*	13·4*	75·5*	13·0*	79·5*	11·2*	93*	10·3*	99*	13·7*	95*	14·3*	85*

January: Forvie, Aberdeenshire — January: Cairn-Monearn, Kincardineshire — A warm February day: Netherley, Kincardineshire — July: hill slopes near Lochinver, Sutherland

* Readings taken amongst mosses. ----- Level of *Calluna* canopy. T(°C.)—Temperature. R.H.(%)—Relative humidity.

Conversely, in winter conditions there may be more loss of heat from the lower parts of the plants and from the ground than in the more complex types of structure, leading to greater fluctuations in the micro-climate at ground level. Similarly, desiccating conditions may prevail more frequently at ground level.

In certain dune heaths, the low *Calluna* bushes become dome-shaped with an exceedingly dense development of the shoots at the periphery, often stimulated by grazing. This canopy is generally formed at only 10-20 cm. above the ground surface, thus enabling the more robust mosses such as *Pleurozium schreberi*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* to grow out to the periphery, intermingling their branches with the shoots of *Calluna*. This fusion of the *Calluna* canopy with the taller of the two moss strata results in so great a reduction of light intensity below (readings as low as 0·02 per cent. have been recorded) that any further colonisation at surface level is excluded. Apart from gaps or thin portions in the canopy, below which *Hypnum cupressiforme*, *Cladonia* spp. and a few others may be present, the ground is covered only by *Calluna* litter and the dead parts of the larger mosses.

In the majority of wet heaths *Calluna*, if present, is variable in height and produces only a weakly developed and open canopy below which *Erica tetralix* and other species may form a stratum at about 20-25 cm., sometimes fairly uniform but never dense. The lack of a dense canopy, together with the more or less permanent supply of ground-water, permits development of a continuous ground stratum usually dominated by *Sphagnum* spp. Relative humidity of the air is thus maintained at high levels close to the ground in spite of the lack of a dense protecting canopy. According to the weather conditions, there is a more or less rapid decrease in humidity on passing upwards. Greater freedom of air-movement obtains in this type of structure than in some of the others, resulting in less appreciable stratification of temperature.

Stratification of root systems

Some information on the spatial arrangement of root systems in certain types of Scottish heathland soils is given by Boggie (1956). Under conditions of free drainage abundant *Calluna* roots are found to a considerable depth as, for example, to the base of a 0·75 m. deep podsol profile in Kincardineshire, with a few penetrating even more deeply between the boulders which form a continuous **C** horizon below. Among mosses or in deep moist litter *Calluna* stems, often procumbent at the base, become buried and give rise to adventitious roots which densely occupy the upper 3 cm. of the soil profile. Between this and a depth of about 10 cm. the larger roots are closely intertwined, while below this level the finer descending roots are rather less concentrated (Plate 41). Roots of *Deschampsia flexuosa* may also extend throughout the full depth of the profile.

A similar pattern is observed in shallower podsolic soils, except that where downwardly growing *Calluna* roots meet an indurated horizon, frequent in Scotland between depths of 60 cm. and 70 cm., they spread out laterally and form a close mat which can be peeled off intact when the loose soil above is removed. This is sometimes also seen just above a thin iron pan (Plate 41).

On dune heaths *Calluna* roots may extend throughout depths of 80 cm., or more, of blown sand, often ceasing only at a junction between the sand and an underlying denser material such as clay or a buried, compacted "fossil" soil. Rhizomes and roots of *Carex arenaria* are frequently closely intertwined with those of *Calluna* down to similar depths, although at the lower levels these are probably dead. A dense stratum of adventitious roots is again evident just below the soil surface, where accumulating blown sand and litter deposited by *Calluna* and mosses surrounds the contorted stem bases.

A strikingly different pattern characterises heaths developing on peat. Here, while species such as *Eriophorum vaginatum* send active roots down to 50 cm. or more, those of *Calluna* are restricted in depth, for example to the upper 20 cm., the majority occupying only the top 5-10 cm. Below this they spread horizontally as if they had come against a barrier, sometimes extending outwards to distances of over 60 cm. It is probable that this limited rooting zone corresponds to the part of the soil lying above a water-table, at least in summer, providing a medium which is aerated and oxidising.

Boggie, Hunter and Knight (1958) have further shown, by the use of radioactive tracers, that in Scottish heaths even where the rooting depth of *Calluna* is considerable, active uptake of ions is very much greater in the upper 10 cm. of soil than below. On mineral soils this applies also to other species of the community, but on deep peat, species such as *Trichophorum cespitosum*, *Eriophorum vaginatum* and *E. angustifolium* show substantial uptake from lower levels.

Floristic Composition of Heath Communities

It is a feature of lowland heath communities that, although there is very considerable floristic diversity resulting in a number of associations, *Calluna vulgaris* is almost always present. It is not necessarily always the dominant, although as already mentioned, this is frequently the case. Very few other species have such a high percentage presence when all types of heath are considered; it may be approached in Scotland by some mosses such as *Pleurozium schreberi*, *Hypnum cupressiforme*,* *Dicranum scoparium* and perhaps *Hylocomium splendens*, but even these may be lacking on the lichen-rich dune heaths.

The abundance of *Calluna* in most heaths has a great influence on the representation of other species, owing to its marked reaction upon the habitat. Besides the influences mentioned in connection with stratification of the communities, *Calluna* deposits litter which, under the Scottish climate, gives rise to a raw humus constituting is in general an acid (pH 3·4-3·9), moisture-retaining, poorly aerated material with a high C/N ratio, in which nitrification is slow. Species which flourish in such a habitat are limited in number: the average of the total number of species, including bryophytes and lichens, in 4 sq. m. samples of seventeen heathland stands was 17. Certain stands occurring on soils of relatively high base status are excluded from this figure; the mean total number of species in five of these was 41. (Figures from McVean and Ratcliffe, 1962.)

* The var. *ericetorum* is widespread, but other forms occur as well. Forms and varieties of this complex species have not been distinguished in the following discussion and Tables.

Details of the several, more or less distinctive, assemblages of species on heaths are given below, but there are certain general features applying to Scotland as a whole. The first of these is the widespread occurrence of *Erica cinerea*, which is a regular component of the communities on all but the wetter soils. This fact alone relates the heaths of Scotland (and Britain in general) to those of the Faeroes, W. Norway, and N. and W. France, rather than to those of Sweden, Denmark, N. Germany, Holland, etc. In other words, Scottish examples belong to the more oceanic groups of heath communities. The frequent occurrence of certain other species, e.g. *Carex binervis*, *Blechnum spicant*, *Listera cordata*, *Dactylorchis maculata* ssp. *ericetorum*, *Plagiothecium undulatum* reinforces this conclusion.

A further feature of the floristic composition of Scottish heaths, resulting from their geographical situation, is that a number of species having northerly types of distribution are frequent while others of southern affinities common on English heaths are generally lacking. So for example, *Trientalis europaea*, *Empetrum nigrum*, *Vaccinium vitis-idaea* and *Hylocomium splendens* are familiar in Scottish heaths; whereas *Ulex minor* and *Cuscuta epithymum* are generally absent. From this angle many Scottish heaths may be related to those of Scandinavia rather than to those of N. Germany, the Low Countries, France, etc., and this is emphasised by the importance of *Vaccinium myrtillus* and *V. vitis-idaea* (also in places *Arctostaphylos uva-ursi*) which indicate affinities with the heaths of S.W. Sweden. An interesting exception to this trend is *Genista anglica* which is prominent in certain heaths of N.E. and N. Central Scotland, as well as in England, while on the Continent it becomes a regular component of heath communities only from N. Germany southwards (Fig. 39, pp. 244, 245). In this respect the Scottish heathland flora shows an interesting parallel to that of the province of Halland in S.W. Sweden, where there is a limited penetration of "southern" species into an otherwise Scandinavian and "northern" assemblage.

Directions of variation in floristic composition

Considerations such as those just mentioned suggest that several distinct trends of variation in floristic composition may be recognisable, each associated with variations in one of the more important environmental factor-complexes ("directions of variation", cf. Sjörs, 1950). Although in the section devoted to Communities (p. 251) an attempt will be made to recognise and describe a number of more or less distinctive "types", heath vegetation presents a complex series of varying combinations of species better regarded as a continuum of variation, the "types" simply representing the more commonly occurring variants. Such variations in floristic composition depend, for example, upon:

(i) differences in the macroclimate between different parts of the country,
(ii) differences in altitude, introducing climatic variations similar to (i),
(iii) local habitat variation with accompanying differences in microclimate and soil factors,
(iv) differences in past history, including past duration of heath vegetation, varying types of management (burning, grazing, etc.).

Treating these in turn, some account may be given of floristic diversity in Scottish heaths.

(i) Certain species rise or fall in abundance, or reach the limits of their geographical range, in relation to climatic gradients between one part of the country and another.

Variation from south to north is seen in the increasing prominence of *Empetrum nigrum*, and perhaps also of *Vaccinium myrtillus*, *V. vitis-idaea*, *Trientalis europaea*, *Cladonia rangiferina*, etc., in the heaths on passing northwards through Scotland. This may be attributed to increasing climatic severity, which is emphasised by the occurrence of species such as *Festuca vivipara*, *Arctostaphylos uva-ursi*, *Empetrum hermaphroditum*,

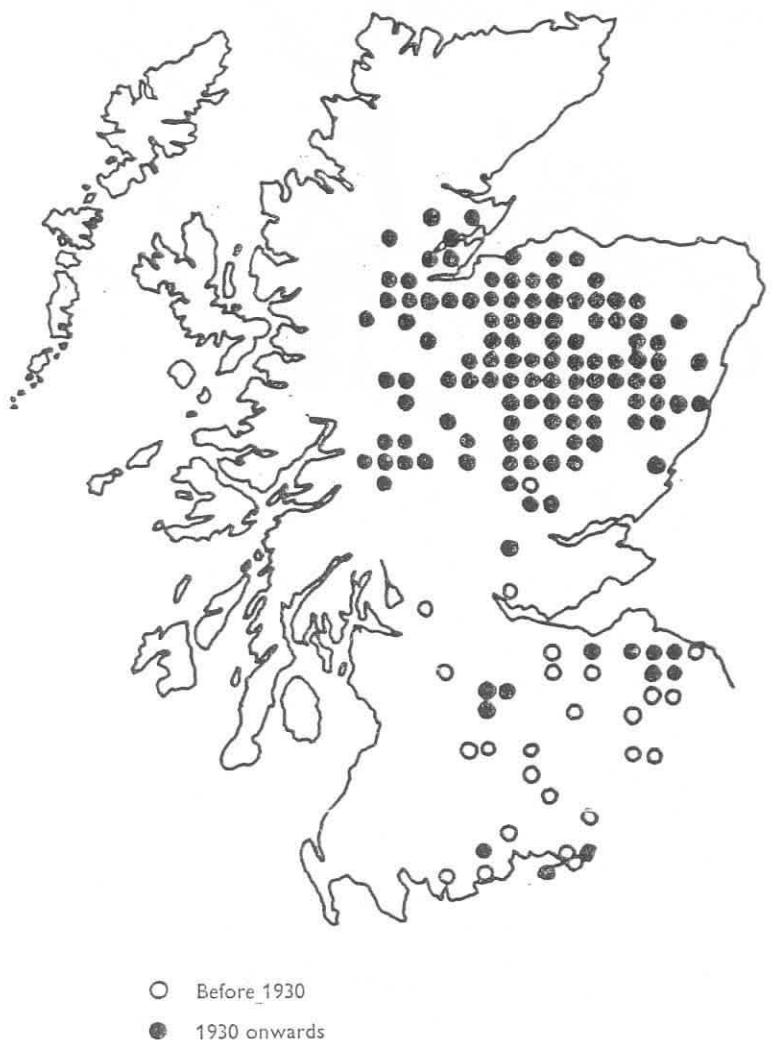


FIG. 39A Scottish distribution of *Genista anglica*. (From: *Atlas of the British Flora*, 1962, p. 100.)

Juniperus communis ssp. *nana*, *Lycopodium selago*, *Cetraria islandica* in heaths at low altitudes towards the north.

Variation which may be related to increasing "oceanicity" of the climate towards the west and the northern coastal regions (with Orkney and Shetland) includes the increased prominence of *Erica cinerea* wherever soils remain freely drained, while *Vaccinium vitis-idaea* and to a lesser extent *V. myrtillus* decline or drop out. *Trientalis europaea* is also more prominent in eastern than western heath communities. Other species illustrating this direction of variation are

FIG. 39B Outline of the general distribution of *Genista anglica*.

Carex binervis, *Hypericum pulchrum*, *Empetrum nigrum*, *Blechnum spicant*, *Dactylorchis maculata* ssp. *ericetorum*, *Selaginella selaginoides*, *Rhacomitrium lanuginosum*, *Rhytidiadelphus loreus* and *Pleurozia purpurea*, all of which become more frequent in heath communities of the more highly oceanic regions. Sample areas in such communities also normally give longer lists of mosses and especially of leafy liverworts. In particular, a number of species largely confined in the east to moist habitats such as woods, damp rocks, etc., appear with some regularity in western heaths: for example, *Dicranum majus*, *Isothecium myosuroides*, *Mnium hornum*, *M. undulatum*, *Thuidium tamariscinum*, *Diplophyllum albicans* and *Frullania tamarisci*. Similarly, species which on the east figure largely in the wetter types of heath community sometimes have a wider ecological range in the west: among these are *Erica tetralix*, *Salix repens*, *Breutelia chrysocoma*, and *Rhytidiadelphus squarrosus*.

(ii) Increasing altitude normally gives rise to a direction of variation similar to that related to increasing climatic severity ((i) above). The cover contribution of the *Vaccinium* spp., for example, frequently increases with altitude, while certain upland species such as *Antennaria dioica*, *Lycopodium selago* and *Juniperus communis* ssp. *nana* may begin to contribute significantly to communities even below the potential forest limit.

(iii) Among "directions of variations" arising from local habitat differences are the following:

(*a*) Changes in community composition on approaching the sea coast. *Festuca rubra*, for instance, becomes a regular component of maritime heaths, while examples very close to the sea may contain *Armeria maritima*, *Plantago maritima* and *Sedum anglicum*, or, where the substratum consists mainly of wind-blown sand as on dune heaths, *Ammophila arenaria* and *Carex arenaria*. A further frequent component of maritime heaths is a group of species indicative of mineral enrichment of the soil (see section (*c*)) such as *Thymus drucei*, *Succisa pratensis* and sometimes *Antennaria dioica*. This enrichment may in some cases come from the deposition of blown sand, but it probably derives also from solutes contained in fine spray and rain from clouds coming in across the sea, especially in the west.

(*b*) Differences in the composition of communities on slopes of differing exposure. Such differences occur where all habitat factors apart from local climate are more or less uniform and are well shown, for example, on the low conical hills of Lewisian gneiss on the north-west coast of Scotland. Examination of a number of stands of *Calluna—Erica cinerea* heath communities on the more freely drained sites below 305 m. (1000 ft.) demonstrated the striking restriction of certain species of the "northern" element of the flora, such as *Vaccinium myrtillus* and *Empetrum nigrum*, to north-facing slopes (Fig. 40). Other species, although less prominent components of the communities, are either similarly restricted or else more numerous on northern than southern slopes, as for example, *Lycopodium alpinum*, *Hylocomium splendens*, *Cetraria islandica* and seedlings of *Sorbus aucuparia*. Bryophytes in general are more prominent on the north sides of hills both as regards number of species and cover contributed. Certain members of the

"oceanic" element in the flora also appear to be more widespread and numerous on northern faces than in corresponding communities with southerly exposure; they include *Blechnum spicant*, *Hypericum pulchrum* and *Rhacomitrium lanuginosum*. Southern slopes are characterised by earlier flowering of species such as *Erica cinerea*.

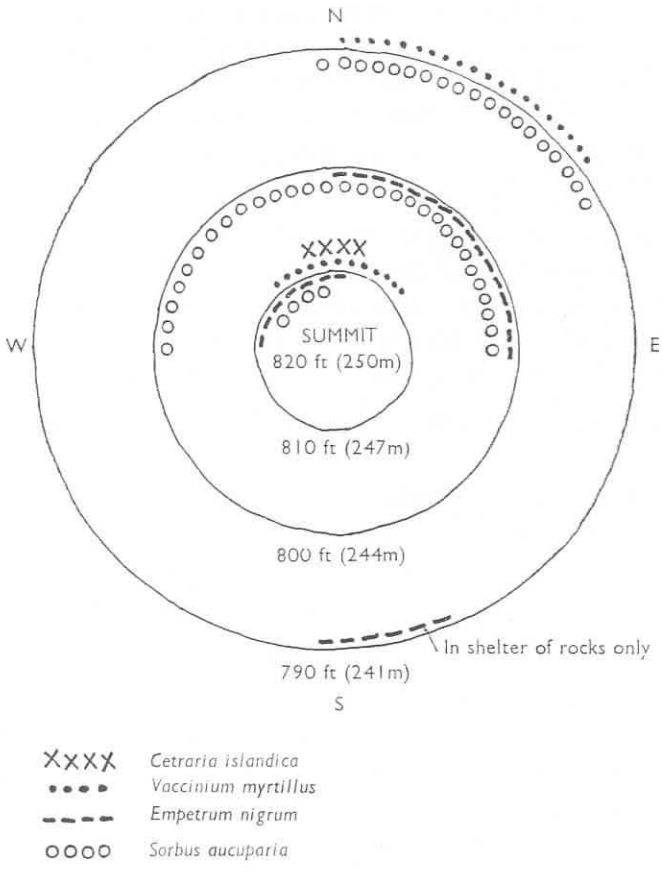


FIG. 40 Diagram illustrating limitation of certain species to the north facing slopes on contours at three altitudes around a symmetrical hill near Lochinver, Sutherland.

(*c*) Variation in soils from types poor in available mineral nutrients to ones which are rather richer. This is accompanied by increasing floristic richness in the community, such that at one end of the range are communities with as few as six species of flowering plants, mainly Ericaceae (but with bryophytes and particularly lichens in addition),

while at the other, numerous species of grasses and herbs may be included of which the following list gives some examples:

Anthoxanthum odoratum	*Euphrasia* spp.
Sieglingia decumbens	*Hypochoeris radicata*
Carex nigra	*Linum catharticum*
Carex panicea	*Polygala vulgaris*
Achillea millefolium	*Prunella vulgaris*
Antennaria dioica	*Succisa pratensis*
Campanula rotundifolia	*Thymus drucei*
	Lotus corniculatus

A few mosses, such as *Pseudoscleropodium purum*, are perhaps also rather characteristic of "herb-rich" heaths.

(*d*) Variation from freely drained soils, through types with impeded drainage, to those which are seasonally or permanently waterlogged. This hydrologic sequence, which may be found on soils derived from almost any parent material, is so frequently repeated in the undulating topography of Scotland that it may be treated as a "soil-vegetation catena" (Fig. 41). The floristic variation usually starts with heaths rich in

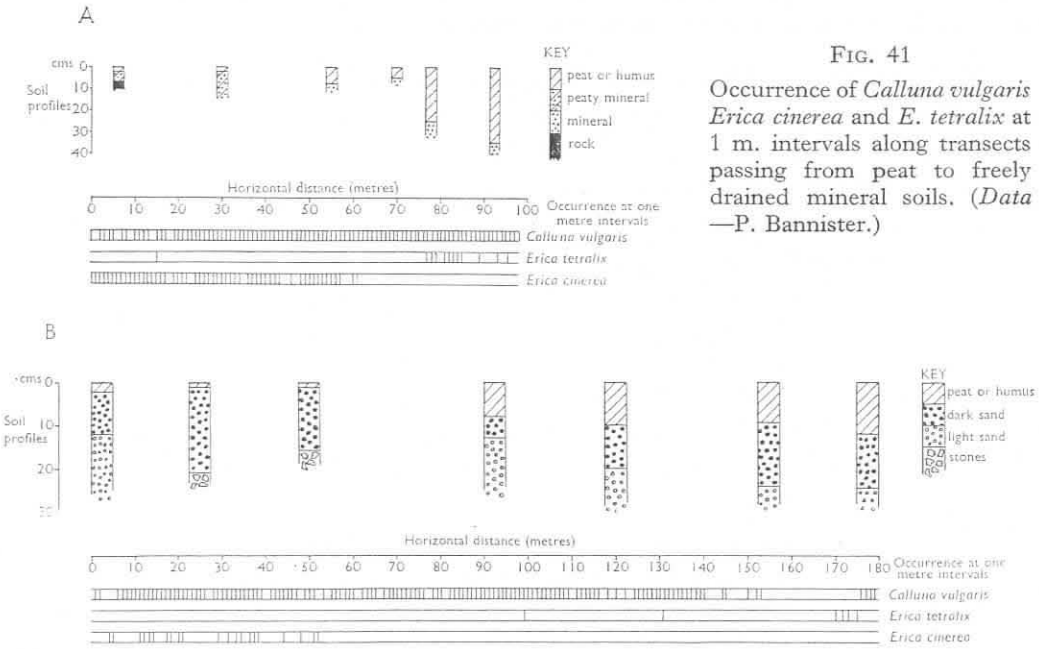


FIG. 41

Occurrence of *Calluna vulgaris* *Erica cinerea* and *E. tetralix* at 1 m. intervals along transects passing from peat to freely drained mineral soils. (*Data* —P. Bannister.)

Erica cinerea on the most freely drained profiles, often admixed with *Calluna*, *Deschampsia flexuosa* and sometimes *Vaccinium myrtillus*. When drainage is impeded, leading perhaps to gleying, *E. cinera* is lacking, *Calluna* is dominant and *Erica tetralix* may enter together with *Juncus squarrosus*. With further deterioration of drainage and increase in the

quantity of water retained in the rooting region, *E. tetralix* increases in abundance, and may be associated with *Molinia caerulea*, *Nardus stricta*, *Pedicularis sylvatica*, *Narthecium ossifragum*, etc. *Calluna* decreases, and is excluded under conditions of prolonged water-logging when a "wet-heath" community results, dominated by *E. tetralix* with *Trichophorum cespitosum*, *Eriophorum vaginatum*, *Myrica gale*, *Carex echinata*, *Polytrichum commune*, *Sphagnum*, etc. This grades into the bog communities characteristic of wet peat. Such sequences, with continuous transition from one end to the other, which may be only a few yards apart or a mile or more, may occur on any heath-covered slope. The same pattern of variation occurs despite differences related to local climate, soil parent material, etc.

(*e*) Certain features of floristic composition are also associated with the variation from soils which are largely mineral in content with a shallow $\mathbf{A}_0$ horizon of raw humus ("hard ground") to those having a considerable depth of organic "top" ("soft ground"—raw humus or peat). It is difficult to separate the effects of these factors from those related to the hydrologic characteristics of the habitat, but *Erica cinerea* for example belongs mainly to soils with little organic accumulation at the surface, and this tendency is shown even more strongly by *Arctostaphylos uva-ursi*. It is brought out again by variation in the bryophytic stratum from communities in which short turf-forming species are prominent to those with dense mat or weft forms, or sometimes *Sphagnum*.

(iv) Variations due to differences in the past history of heathland areas may be separated into those dependent largely on the time-interval since the origin of the community and those related to management practices.

(*a*) Certain aspects of floristic composition may vary with the time-interval since the initial derivation of heath from forest. "Younger" heaths may be rich in shade-tolerant species such as *Deschampsia flexuosa* and other indicators of woodland conditions (a possible example being the beautiful moss *Ptilium crista-castrensis*, a local component of Scottish heaths), while in longer-established communities there has been ample time for the entry of species excluded from forest, e.g. *Erica cinerea*, and suppression of the grasses. It has often been held that the occurrence of species such as *Anemone nemorosa*, *Oxalis acetosella* and *Polypodium vulgare* in heaths is a sign of recent derivation from woodland, but they also occur in long-established heaths both in Scotland and on the Continent, as well as at altitudes above the normal limit of forest.

(*b*) Grazing. Detailed observation and experiment on the influence of grazing animals has been largely confined to sheep. With increasing grazing intensity the dominance of *Calluna* is at first enhanced (under relatively mild grazing) so that its increasing cover tends to exclude other species including *Erica cinerea* (Gimingham, 1949). Many herbaceous species are also progressively eliminated, and this factor may account partially for the scarcity of species such as *Polypodium vulgare*. Thus, Spence (1960) has pointed out that in South Uist and Shetland, *Polypodium* is a regular component of the vegetation of ledges and islands in lochs, which are not subjected to grazing and burning. Further increase in grazing intensity damages *Calluna*, which may be

eliminated in favour of grasses. This change (cf. Tansley, 1949) takes place more readily on base-rich soils where a productive pasture composed, for example, of *Festuca ovina* with *Agrostis* spp., etc., may result, but where *Pteridium aquilinum* is present in the area it may be given the opportunity to spread to serious proportions. Alternatively, on acid, base-poor soils *Deschampsia flexuosa* may increase and some surface erosion may take place in dry habitats, while in wet conditions *Nardus stricta*, *Molinia caerulea* or *Trichophorum cespitosum* may become dominant in almost pure stands.

Cattle and deer also contribute to the effects of the grazing factor on the composition of moorland communities. They may be responsible for the failure of tree-seedling establishment and, along with burning, for the very localised occurrence of shrubs such as *Juniperus communis*, so prominent a feature of N.W. European heaths (cf. also Chapter 6).

(*c*) Burning. Directions of variation resulting from the occurrence of fire depend upon its intensity (the temperatures reached) and frequency. A single very hot fire, in which the whole vegetation is destroyed and the surface humus or peat ashed down to depths of 10 cm. or more, may entirely alter the composition of the vegetation for many years. The temperatures produced in such fires, starting accidentally or from failure to control a routine burn in dry windy weather, have never been measured, but they certainly exceed 800°C. The organic horizon of the soil may be destroyed over considerable areas, erosion gulleys may form, and colonisation of the sterilised, leached mineral surface may be very slow. One such area in Inverness-shire examined five years after the fire, had the following community:

> *Polytrichum juniperinum* and *Ceratodon purpureus* (co-dominant).
> *P. piliferum* and *P. commune* (frequent).
> Occasional plants of *Calluna vulgaris*, *Agrostis tenuis*, *Deschampsia flexuosa*, *Festuca ovina*, *Juncus squarrosus*, *Nardus stricta*, *Carex nigra*, *Anthoxanthum odoratum*, *Rumex acetosella*, *Aira praecox*.

In time, however, it may be presumed that there would be renewed formation of a raw humus horizon and a heath community would return.

In the well-controlled fires employed in the management of many heathlands, temperatures just above ground surface seldom exceed 800°C. and normally fall between 300°C. and 500°C. (Whittaker, 1961). The practice of burning at more or less regular intervals, however, may cause more permanent differences in the flora than the occasional severe fire. With extremely frequent fires (e.g. at intervals of from one to six years), the heathland community characteristic of any particular region of Scotland may be modified by the elimination of all herbaceous species lacking buried perennating organs. Even such species as *Vaccinium vitis-idaea* may be lost, and the dominance of *Calluna* reduced, since although it regenerates readily after fire it is not amongst the species which re-establish cover most rapidly. Consequently *Pteridium aquilinum* (cf. p. 273), *Vaccinium myrtillus*, *Nardus stricta*, *Molinia caerulea*, and *Juncus squarrosus* may be among the

invaders, according to the moisture regime of the habitat. Certain other resistant species may multiply, including *Carex pilulifera* and other *Carex* species, *Blechnum spicant*, etc.

This type of community grades into those produced by a less frequent burning routine, with intervals often of eight to fifteen years between fires. This is normal burning practice, designed to maintain the dominance of *Calluna* at its maximum. It leads to the progressive elimination not only of species most sensitive to fire but also of those sensitive to competition with *Calluna*. Almost pure stands of *Calluna*, with few associates other than bryophytes and lichens, may be produced over large areas. Still longer intervals between fires permit a richer floristic composition to be maintained approaching that of unburnt areas in the same district.

The actual floristic composition of Scottish heathland communities is, therefore, a product on the one hand of climatic and edaphic factor-complexes varying in different directions across the country and, on the other, of varying intensities of influences exerted directly or indirectly by man both at present and in the past. The composition of any particular community can be interpreted fully only with reference to all these influences. In this type of vegetation perhaps more than in most others the chances of similar groupings of controlling factors occurring in many distinct localities are low. The variation in community composition is correspondingly great, and may be in the nature of a more or less continuous network of trends. Any particular example of a heathland community may be regarded as occupying a point on this network, with related types occurring along the numerous different directions of variation produced by gradients in the various controlling factors.

The Communities

Despite what has just been said it remains possible to compare the composition of many examples of Scottish heathland communities and to group those which are most alike. Amongst the first to attempt this was W. G. Smith (1905, 1911) who suggested the following simple scheme:

HEATHER ASSOCIATIONS:

(*a*) Heath or dry heather moor (Heide) where *Calluna vulgaris* occurs with *Erica cinerea* and associates which prefer dry soils.

(*b*) Heather moor (Heide moor) thoroughly dominated by *Calluna vulgaris* and associates preferring a slight depth of peat:

(i) exclusively *Calluna*, often on sloping ground;

(ii) *Calluna* and *Erica tetralix*, peat deeper and moister.

(A "mixture of Grass Heath and Heather Associations" is also recognised.)

In establishing these groups, reference was made both to the chief dominants and to an aspect of the habitat—the nature of the substratum. Tansley (1949), however, took the view that there was "no good vegetational distinction" between "*Calluna* heath" and "*Calluna* moor" (as described by Smith) but, as can now be shown, Smith had merely

picked on one "direction of variation", that which occurs on passing between "hard" and "soft" ground. Tansley, contrasting "upland heaths" with "lowland heaths", emphasised the altitudinal "direction of variation". Both treatments are, however, inadequate for the purpose of establishing a convenient grouping of those communities which are most alike and occur in similar habitats.

In 1940 Muir and Fraser, by detailed description of the heath communities in a restricted area of Aberdeenshire, produced a useful grouping of heath communities based on the leading dominants. While recognising that it was impossible to tell how far this scheme would apply to other parts of the country, Zehetmayr regarded it as the most complete description of Scottish heath vegetation available to him in 1960 for his bulletin on "Afforestation of Upland Heaths", and he summarises it as follows:

DRY HEATH TYPES:

Calluna—Erica cinerea

Calluna with abundant *Erica cinerea* forming the ground cover, subsidiaries not very frequent and usually suppressed.

Calluna—Vaccinium myrtillus

Calluna dominant, with abundant *V. myrtillus* co-dominant; *V. vitis-idaea* generally frequent.

Calluna—Arctostaphylos

Calluna dominant but open. Undergrowth of *Arctostaphylos*. Many subsidiaries.

Calluna—Deschampsia—Vaccinium myrtillus

Calluna dominant but open; subdominant or locally co-dominant *Deschampsia flexuosa* and *Vaccinium myrtillus*.

MOIST HEATH TYPES:

Calluna—Deschampsia flexuosa

Calluna dominant, with occasionally flowering, partly suppressed *D. flexuosa* abundant. Turf usually quite covered.

Calluna—Vaccinium

Calluna dominant, with suppressed or poor growth of *V. myrtillus* and *V. vitis-idaea* abundant. Turf exposed and showing growth of encrusting lichens.

Calluna—Nardus

Calluna normally dominant, with *Nardus* sub-dominant or co-dominant. *Pleurozium schreberi* the chief moss, along with patches of *Sphagnum*.

Submoorland types

Variable subtypes characterised by the presence of peat, subsidiary and co-dominant plants such as *Erica tetralix*, *Eriophorum vaginatum*, *Trichophorum cespitosum*, *Carex* and *Juncus* spp. abundant or locally abundant. *Sphagnum* spp. and *Pleurozium schreberi* usually the most frequent mosses.

EXPOSURE TYPES:

(Details of "Dry Eroded *Calluna*" and "Wet *Calluna—Cladonia*".)

It is now possible to suggest a more comprehensive scheme of groups, resulting from the scrutiny of tables recording the floristic composition of some 300 sample areas of heathland stands in Scotland. Since, as indicated above, these communities exhibit more or less continuous variation, grouping is at best an arbitrary division. Different arrangements could be adopted with equal success while transitional examples between groups will always occur. However, the following groups each incorporate those stands in which the chief species (i.e. those with quantitatively the largest contribution) are substantially the same, and the lists of associated species, although variable, show greater affinities than differences.

Since communities having sufficient floristic similarity to be placed in the same group can only occur where broadly similar habitat conditions prevail, a grouping of this kind should be of some service when vegetation is to be used as an indication of habitat potentialities. It will also express the climatic and geographical affinities of the community type, since each group will contain different proportions of species having essentially northern, southern, oceanic, continental and other distribution patterns. Bøcher (1943) surveyed the whole North Atlantic Heath Formation on this basis and it is convenient to list Scottish groups (some of which coincide with his) under his main headings—the "Euoceanic Series" and the "Scano-Danish (Scotch) Series".

Euoceanic Series

This title was given by Bøcher to heath communities occurring along the highly oceanic seaboard of western Europe, all of which contain a relatively high proportion of species showing "oceanic" patterns of distribution. At least two rather distinctive types appear in Scotland.

***Calluna—Empetrum hermaphroditum* communities.** A convenient starting-point for a survey of some of the main groups into which Scottish heaths can be divided on floristic grounds is provided by one representing some of the extremes of variation to be found at low altitudes. On the islands in certain Lochs in Shetland, Spence (1960) has found and described examples of communities dominated by *Calluna*, with *Empetrum hermaphroditum* playing a prominent role (Table 25, p. 280). *E. hermaphroditum* enters into low-lying heath communities elsewhere in Shetland and in the Hebrides (e.g. South Uist: Spence, 1960), but on the level plateaux of peat characteristic of the centres of these islands in Shetland lochs it is a regular member of a type of community including other species of markedly northern, submontane affinities, as well as a strong oceanic component. Among the former are *Juniperus communis* ssp. *nana*, elsewhere in Britain belonging largely to mountain heaths ("Juniperetum nanae", McVean and Ratcliffe, 1962), *Euphrasia scottica*, *Vaccinium vitis-idaea* and *V. uliginosum*. The high constancy of *Potentilla erecta* (100 per cent.) and to a lesser extent of *Deschampsia flexuosa* (83 per cent.) are also features of northern heath-types (see Gimingham, 1961). Among the oceanic components are *Blechnum spicant* (32 per cent.), *Carex binervis* (50 per cent.), and *Rhacomitrium lanuginosum* (32 per cent., locally dominant). *Erica cinerea*

however, is sparsely and irregularly represented, and this, together with the high constancy of *Rhinanthus minor* agg. and the montane element, appear to be among the features differentiating this from other Euoceanic heath community-types.

Altitudinal and edaphic range. The lochs with islands on which these communities are represented are situated at altitudes ranging from 8 to 150 m. above sea-level. The substratum is peat over 1 m. in depth, overlying boulders or bedrock of sandstone or granite-diorite.

Distribution. In the form described this community appears to be restricted in Scotland to Shetland. However, further surveys may reveal similar communities in the north-west coastal region and islands. Some of the characteristics mentioned above might then prove to be local features of the Shetland examples.

Relationship to other communities. These communities are clearly related to the *Vaccinium—Empetrum hermaphroditum* communities so common above the tree-line on Scottish mountains (cf. Chapter 11). Indeed, as Spence demonstrates, mean monthly temperatures at sea-level in Shetland are equivalent to those at 359 m. in the central Highlands, and those at 305 m. in Shetland equivalent to 762 m. in the central Highlands. The climate in which the communities under discussion develop may, therefore, properly be described as sub-alpine, and relationships with other sub-alpine communities are to be expected. Their situation, however, at low altitudes on an off-shore archipelago with a more oceanic climatic regime than that of the central Highlands introduces relationships with the other oceanic heath types (see below) and, together with the northerly geographical situation, produces a marked similarity to certain heaths in the Faroes (Bøcher, 1940). Here, a *Calluna—Empetrum* (*E. nigrum* and *E. hermaphroditum*) type of community very similar to the Shetland ones has been described. It is, however, often rich in *Vaccinium myrtillus* and so relates in turn to the *Empetrum—Vaccinium* heaths of the Faroes and, for example, South Greenland.

Ecological history. It is striking that in Shetland these communities are virtually confined to islands in lochs, which have largely escaped the influence of grazing and burning. In the neighbouring moorland, subject to the effects of these factors, *Empetrum hermaphroditum* plays a less important part while *Erica cinerea* becomes more prominent, and a community similar to the *Calluna—Erica* type described below results, but lacking *Juniperus*, *Polypodium vulgare*, *Rhinanthus minor*, etc. Alternatively, wetter conditions lead to the prominence of *Trichophorum cespitosum*, *Eriophorum* spp. and *Molinia caerulea*.

***Calluna—Erica cinerea* heaths,** containing numerous species with oceanic affinities. The dominant is sometimes *Erica cinerea*, usually *Calluna* with abundant *E. cinerea*. These communities, widespread in the coastal and oceanic parts of Scotland, exhibit *Erica cinerea* at its most vigorous, usually in association with *Calluna*, but with *Empetrum* and *Vaccinium* spp. only occasionally represented and then in relatively small quantities (Table 25). As in the preceding type, *Potentilla erecta* is highly constant, and *Agrostis* spp. (especially *A. tenuis*) are regular components. *Hypnum cupressiforme* is of chief importance amongst the mosses, with *Dicranum scoparium* and *Hylocomium*

splendens frequently well represented. *Pleurozium schreberi*, however, is abundant only in a few examples and may be sparse or lacking. Lichens are poorly represented. Among the oceanic species which either reach relatively high levels of constancy, or else are abundant when present, are *Blechnum spicant*, *Hypericum pulchrum*, *Carex binervis*, and *Dactylorchis maculata* ssp. *ericetorum*. Numerous others, especially bryophytes, figure in the list although their occurrence is less regular.

Variants include :

(α) "*Herb-rich*" *variants*. A number of examples of heath communities showing the characteristic features of this group include also better representation of a series of herbaceous species generally regarded as indicative of soils in the medium to higher ranges of base-status (e.g. *Antennaria dioica*, *Anthoxanthum odoratum*, *Euphrasia* sp., *Hypochoeris radicata*, *Sieglingia decumbens*, *Solidago virgaurea*, *Succisa pratensis*, *Thymus drucei*, *Pseudoscleropodium purum*). The stands contributing to column 3 in Table 25 include examples from semi-podsols developed over somewhat calcareous schist, and in maritime localities from soils enriched by wind-blown beach sand or perhaps by rain water brought in with westerly winds from over the Atlantic (cf. Gorham, 1956). The presence of *Armeria maritima* and *Plantago maritima* in certain stands probably reflects the influence of the latter factor.

(β) "*Dune heath*" *variants*. Certain west-coast sand-dune systems are highly calcareous (Chapter 4), but there are also numerous others in which the succession on the older, fixed dunes and on fixed flat expanses of blown sand leads to dune heath. Here, *Erica cinerea* may be the pioneer dwarf shrub (Plate 42), sometimes producing large dome-shaped bushes scattered amongst *Ammophila*, well before it is joined by *Calluna* and the separate shrubs coalesce to form *Calluna—Erica* communities essentially similar to those discussed above (Table 25, col. 4). This behaviour of *Erica cinerea* under highly oceanic climatic conditions provides a strong contrast to its reduced role in otherwise similar dune systems on the east coast, where *Calluna* or sometimes *Empetrum nigrum* may be the pioneer dwarf shrub (cf. pp. 257 and 264).

The dune-heath communities rich in *Erica cinerea* tend also to be more or less "herb-rich", reflecting perhaps both the relatively favourable base-status of the blown sand and the maritime situation. Species such as *Lotus corniculatus*, *Viola riviniana* and *Veronica officinalis* are regular. These communities, however, are to some extent distinguished from the rest by such plants as *Ammophila arenaria* (although usually in a more or less degenerating condition), *Carex arenaria*, *Festuca rubra* and *Rhytidiadelphus triquetrus*, these species being characteristic of dune heaths in general (see also p. 264).

Altitudinal and edaphic range. Most of the examples of this group which have been examined belong to low altitudes ranging from the dune heaths at a few metres above

sea-level to about 90 m. Some of the "herb-rich" representatives are developed at higher altitudes, in relation to the occurrence of base-rich soil parent materials, e.g. up to 350 m. The substratum varies from blown sand with a slight admixture of humus, through shallow unstratified brown soils with deep-burrowing earthworms, to shallow podsolic soils in which, however, the surface layer of raw humus (A_0) is never thick, seldom exceeding 5 cm., and leaching is not pronounced. As shown above (p. 255), *Erica cinerea* is favoured by freely drained soils.

Distribution. Heaths of this group occur mainly close to the north and west coasts and in the outlying islands, but also scattered here and there in suitable localities elsewhere in the country.

Relationship to other communities. Relationship with *Calluna—Empetrum hermaphroditum* heaths has already been indicated. The Scottish Euoceanic *Calluna—Erica cinerea* heaths bear a very close relationship to similar communities in the hyperoceanic region of W. Norway (e.g. in the region of Haugesund and Jaeren peninsula: Nordhagen, 1921; Bøcher, 1940; Gimingham, 1961) and to closely comparable ones in the Faroes (Bøcher). In the opposite geographical direction they merge gradually into the *Calluna—Erica cinerea—Ulex gallii* heaths of Wales; while within Scotland various communities containing both *Erica cinerea* and *Vaccinium* spp. in appreciable quantities, or both *E. cinerea* and *Arctostaphylos uva-ursi*, link the Euoceanic to the Scano-Danish (Scotch) Series.

The "herb-rich facies of Callunetum vulgaris" described by McVean and Ratcliffe (1962) can be regarded as identical with the herb-rich variant of the Euoceanic *Calluna—Erica* heaths described here.

Ecological history. The origin and development of heaths rich in *Erica cinerea*, apart from those on sand dunes, have been little investigated. It is well known that, where present, the contribution of *E. cinerea* to heath vegetation is increased, at least temporarily, after burning. This may follow perhaps from the drying out and improvement of drainage and aeration of the surface soil layers following fires. It is possible, therefore, that burning may be a factor concerned in the wide-spread occurrence of this type, especially where examples lie outside the most oceanic parts of the country. Any factors which reduce the competitive vigour of *Calluna* and retard the development of raw humus at the soil surface favour *Erica cinerea*, and this relates presumably to the association of this group of communities with oceanic regimes, and with relatively base-rich soils. On the other hand, factors such as sheep grazing of moderate intensity, which enhance the competitive effects of *Calluna*, will reduce *E. cinerea* (Gimingham, 1949). On the more fertile soils heavier grazing tends to eliminate both species, and many *Calluna—Erica cinerea* communities can be replaced by grassland under appropriate management.

Scano-Danish (Scotch) Series

Certain of the heaths reaching their optimal development in south-west Scandinavia show close affinities to those of the rather less highly oceanic parts of Scotland. The series

so constituted was given the above title by Bøcher, distinguishing it from the Dutch-German Series and the Baltic-Submontane Series.

Scottish representatives of this series appear to fall conveniently into four groups (Table 27, p 288).

***Calluna—Erica cinerea* heaths** with the oceanic floristic element reduced, but in which *Vaccinium* spp. are absent or insignificant.

Communities of this kind, occurring fairly frequently in the eastern half of Scotland, may be regarded as occupying a more or less intermediate position between the oceanic *Calluna—Erica cinerea* heaths, and the widespread *Calluna—Vaccinium* heaths (below, p. 258). Indeed, they may in several instances merely represent versions of one of these community-types impoverished by frequent burning and regular grazing. This view is further supported by the fact that they show few distinctive floristic features, and, apart from an occasional "herb-rich" example, are poor in species of flowering plants. Besides *Calluna* and *Erica cinerea* the only species occurring with some regularity are *Carex pilulifera* and *Trichophorum cespitosum*; even *Potentilla erecta* is no longer so regular or important a component (Table 27, col. 1). Mosses may be well represented, and when this is so the balance is similar to that described above for the oceanic *Calluna—E. cinerea* heaths, with *Hypnum cupressiforme* of chief importance. In other examples, lichens, especially *Cladonia pyxidata*, are widespread.

Variants include:

(a) *Stands dominated by* Calluna vulgaris *alone* (Table 27, col. 2). Further reduction in the community structure is observed when *Calluna* is dominant in almost pure stands, having no associated dwarf shrubs. Such communities occur frequently, especially in east Scotland, but also for example on dunes in the west. Most commonly they belong to heaths in the agricultural lowlands, now surrounded by farmland and often restricted in area by reclamation. This suggests that they may have been much modified in the past; in many cases they have been frequently burnt. The absence of *Erica cinerea* may be due either to somewhat poorly drained or peaty soils reducing its competitive vigour in relation to *Calluna*, or to grazing or other factors enhancing the dominance of *Calluna* to the virtual exclusion of all else. Other features of the flora of these communities bear a similarity to those described in the preceding paragraph, as for example the leading role of *Hypnum cupressiforme* among the mosses, while both *Pleurozium schreberi* and *Hylocomium splendens* are sparse. It seems appropriate, therefore, to treat these types together, although it is not suggested that all communities in which *Calluna* is the sole representative of the dwarf shrubs have originated in the same way or bear the same relationships to other groups. Indeed, it is highly probable that similar communities may be derived from former *Calluna* with *Vaccinium* heaths by the operation of the factors mentioned. (The "Callunetum vulgaris" of McVean and Ratcliffe (1962) contains stands referable

here, although the majority relate to the *Calluna—Vaccinium* heaths, see below.) It is difficult to regard these communities as anything more than much modified or reduced versions of related types, or intermediates between the more clearly recognisable groups, occupying habitats which are neither strongly oceanic nor suitable for the other typical associates of *Calluna*, such as *Vaccinium* spp., *Arctostaphylos uva-ursi* or *Empetrum nigrum*.

(β) *Calluna* with *Erica cinerea* and *Arctostaphylos uva-ursi* (Table 27, col. 3). Examples are met with in parts of the eastern foothills of the Grampian and Cairngorm massifs, and perhaps elsewhere, combining the features of the heaths placed in this section with strong representation of *Arctostaphylos uva-ursi* (Plate 38). They lack, however, the very typical assemblage of species which characterise the *Calluna* with *Arctostaphylos* communities described as a distinct main type below. Indeed, *Calluna*, *Erica cinerea*, *E. tetralix*, *Arctostaphylos uva-ursi* and *Hypnum cupressiforme* are the only species which appear to reach high constancy values in the rather small set of samples examined, and this suggests again that these are probably to be regarded as transitional stands between the *Calluna—Erica cinerea* and *Calluna—Arctostaphylos* types or as reduced versions derived from one or the other. One stand in which *Vaccinium myrtillus* is frequent suggests a possible relationship with *Calluna—Vaccinium* heaths.

Edaphic range. These communities are found mainly on "hard ground". There is frequently a thin accumulation of litter and raw humus, up to about 5 cm. in depth, overlying a shallow mineral profile which may be clearly or obscurely podsolised (podsol ranker). Sometimes the organic top may rest directly on stony till or rock debris decaying *in situ* (ranker). A few examples on peat have been noted, where the surface has become thoroughly drained and is no longer moistened by a ground-water table.

***Calluna—Vaccinium* heaths, usually including *Empetrum nigrum* and often also *Erica cinerea*.** This group of heath communities is probably the most important and characteristic of Scotland as a whole. It is extremely widespread, occurring in suitable habitats throughout the whole country, and frequently extends in one form or another over large areas (Plate 37). Many of the best grouse moors and hill grazings belong here. Typically, *Calluna* is dominant but both *Vaccinium myrtillus* and *V. vitis-idaea* are regularly present in varying quantities (Table 27, col. 5). *Erica cinerea* no longer plays the part it has in the preceding groups, although it is often present in a subordinate status, sometimes actually forming a discontinuous lower stratum below the canopy of *Calluna*. *Empetrum nigrum* becomes a component of high constancy, but its bulk and cover are seldom great. Other general features are the regularity with which *Deschampsia flexuosa* occurs, and the reduced role of *Potentilla erecta*, *Agrostis* spp., *Blechnum spicant* and other species prominent in one or more of the preceding groups. Chief among the mosses is now *Pleurozium schreberi*, with *Hypnum cupressiforme* very regularly accompanying it but quantitatively in second place. *Hylocomium splendens* is

also a characteristic species of high constancy; *Dicranum scoparium* and *Polytrichum commune* are slightly less regular. Lichens, although not prominent, are generally represented, particularly by *Cladonia sylvatica* and *C. uncialis*. Additional bryophytes becoming constant in certain western examples of this heath type are *Plagiothecium undulatum*, *Anastrepta orcadensis*, *Bazzania tricrenata* and *Scapania gracilis*.

The proportions in which the two *Vaccinium* spp. occur vary but, at least in the lowland heaths, examples in which *V. vitis-idaea* is present but *V. myrtillus* is absent are rare. On the other hand, heaths containing *V. myrtillus* extend well beyond the range of conditions in which *V. vitis-idaea* plays a part, especially towards the oceanic west. For this reason, some authors such as Bøcher (1943) have preferred to constitute a community-type based on strong representation of *V. myrtillus* (the "Myrtillion boreale"), with *V. vitis-idaea* as an additional component in examples from certain parts of the geographical range. However, Scottish experience suggests that heaths with both *Vaccinium* species represent the fullest expression of this community-type, which should therefore be described in these terms. Those with only one of the two species may then be treated as variants occurring under conditions which eliminate the other.

Variants include:

(α) Calluna *with* Vaccinium myrtillus; V. vitis-idaea *absent* (Table 27, col. 5). In these examples *Erica cinerea*, although not more than about 57 per cent. constant, is often abundant. *Potentilla erecta* is also perhaps rather better represented than is often the case in the heaths with both *Vaccinium* species. Otherwise the general description given above applies equally here.

(β) *Communities dominated by* Vaccinium myrtillus, *in which* Calluna *is reduced or lacking*. In lowland regions *V. myrtillus* is seldom dominant, but patches of limited extent occur in which other dwarf shrubs are suppressed or excluded. These sometimes mark the site of former woodland and are then of a temporary nature, but they occur in heathland by rock outcrops, and especially among large boulders or scree with deep crevices. Sometimes *V. myrtillus* also becomes dominant on very exposed ridges or ledges (cf. Pearsall, 1950: "*Vaccinium* edge"), or, perhaps temporarily, as a result of overburning when the vigour of *Calluna* is reduced (Elliott, 1953).

Variations in soil conditions may also produce variants in community composition, as in previous types. The following are among the most distinctive variants:

(γ) *Herb-rich variants*. On the richer soils, communities of the *Calluna* with *Vaccinium* spp. type may show a flora enriched with additional species, such as those mentioned in connection with similar variations in the *Erica cinerea* heaths. However, perhaps in view of the soil conditions normally associated with *Calluna—Vaccinium* heaths this does not here seem to be such a pronounced tendency.

(δ) *Moist variants*. A number of examples, however, contain an important component of species otherwise characteristic of wet heaths. These are

clearly transitional between the *Calluna—Vaccinium* type of community and certain of the wet heaths developed in otherwise similar sorts of habitat (cf. p. 265 and Chapter 10). In some cases *Trichophorum cespitosum*, *Juncus squarrosus* or *Eriophorum vaginatum* are among the prominent species, and along with them *Erica tetralix* and *Sphagnum* spp.; while more occasionally *Nardus stricta*, *Molinia caerulea*, *Pedicularis sylvatica*, *Rubus chamaemorus* and *Aulacomnium palustre* are associated.

Altitudinal and edaphic range. Communities containing *Calluna* and both species of *Vaccinium* occur in mountainous regions up to altitudinal limits varying between 750 m. and 1850 m. (cf. Chapter 11 and Metcalfe, 1950). Many of these are essentially similar to the types described here, incorporating, however, some additional montane species (such as *Chamaepericlymenum suecicum*, and *Empetrum hermaphroditum* in place of *E. nigrum*). The features of floristic composition given in this section apply largely to examples lying below about 600 m., but there is no sharp distinction from those at higher levels. There is no lower altitudinal limit, examples of this community-type occurring down to sea-level. However, below about 100 m. on the east side of Scotland and 360 m. on the west, *Vaccinium vitis-idaea* is normally excluded and the variant containing *V. myrtillus* only occurs.

Although this community-type is represented over a considerable range of soil moisture conditions, in other respects the soil-type is rather clearly defined. It is one in which there is an appreciable depth of raw or peaty humus, and so ranges only from drained or drying peat to podsol rankers, semi-podsols and podsols. Most characteristic of these is thin peat over a podsol with thin iron pan, but other substrata include truncated podsols and stabilised scree with accumulated raw humus in the crevices, as well as podsolic gleys. These soils are invariably acid, the pH at the surface normally falling within the range 3·6-4·5.

Towards the wetter extremes of this edaphic range species typical of wet heaths increase in prominence, producing communities of the type described as moist variants (δ); where a parent-material of slightly higher base-status leads to a less markedly podsolised profile with a shallower $\mathbf{A}_0$ horizon, herb-rich variants may arise (γ).

Distribution. Widespread in the hilly districts of Scotland, and in the lowlands where soils are relatively acid and of low base-status. The complete version, with both *Vaccinium* species, is most frequent in north, east and central Scotland, and elsewhere at the higher altitudes. The variant containing *V. myrtillus* only, however, extends into all the lowland and coastal regions and in the west is also prominent on the hills.

Relationship to other communities. Scottish *Calluna—Vaccinium* communities are closely similar in composition to an important heath-type in western Sweden, extending also into S. Norway, Denmark and more isolated stations, e.g. on north-facing slopes, in N. Germany and Holland. In these areas the leading species are the same as those in Scotland with a few important differences. Chief among these is the absence on the Continent of certain oceanic species, especially *Erica cinerea* and *Blechnum spicant*, and

the presence of a small number of more Continental species, lacking in Scottish heaths, such as *Arnica montana*, *Scorzonera humilis* and *Dicranum rugosum*. Otherwise the floristic composition, including that of the bryophytic stratum, of examples from the two regions is closely similar. Damman (1957) examining the Swedish examples, named them "Hylocomieto—Callunetum", giving prominence to the role of *Hylocomium splendens* in the bryophyte stratum. This is broadly a northern-oceanic species and serves to differentiate these communities from more southern or Continental heaths. Among other species used to differentiate the Swedish "Hylocomieto—Callunetum" from more southern heath-types, the following also occur in the equivalent Scottish communities: *Luzula pilosa*, *Cladonia rangiferina*, *Lycopodium clavatum*, *L. selago*, *Trientalis europaea*, *Anemone nemorosa*. It is reasonable to regard the Scottish type as a somewhat more oceanic version of the Scandinavian.

Since the range of the *Calluna—Vaccinium* heaths overlaps that of the highly oceanic *Calluna* with *Erica cinerea* communities in Scotland, there is intergradation between them and many transitional examples are found which could readily be placed in either group, with *E. cinerea* normally contributing considerable cover. In other cases, *Calluna* is overwhelmingly dominant, with other dwarf-shrubs contributing little cover. Recognising that, at least in heaths situated below the natural tree limit, this may be a result of anthropogenic factors, McVean and Ratcliffe (1962) placed all such stands from the Highland region in a single "Callunetum vulgaris" based on the dominance of *Calluna* and the constancy of *Dicranum scoparium*, *Hylocomium splendens*, *Hypnum cupressiforme* and *Pleurozium schreberi*. Most of the stands listed in their table could clearly be associated with the *Calluna—Vaccinium* heaths described above since they contain varying quantities of *Vaccinium* spp., while a few seem to link with the variant (α) of *Calluna—Erica cinerea* heaths (p. 257).

At higher altitudes the communities described in this section grade into the "Vaccinieto—Callunetum" of McVean and Ratcliffe.

***Calluna—Arctostaphylos* heaths, with *Erica cinerea* and often *Genista anglica*, *Pyrola media*, *Lathyrus montanus*, etc.** Certain heaths from the upland regions of central and eastern Scotland in which *Calluna*, *Arctostaphylos uva-ursi* and *Erica cinerea* figure prominently, contain also a number of interesting species not regularly found in other heath types. Indeed, the basic assemblage of species is so strikingly similar from stand to stand, even in widely separated areas, that this community-type is one of the most clearly defined and readily recognisable among the heaths, contrasting with the variable nature of those hitherto described. Among the most constant species are *Agrostis tenuis*, *Deschampsia flexuosa*, *Festuca ovina*, *Lathyrus montanus*, *Lotus corniculatus*, *Potentilla erecta*, *Pyrola media*, *Vaccinium vitis-idaea*, and of the mosses *Hypnum cupressiforme* is again the chief species, while both *Pleurozium schreberi* and *Hylocomium splendens* are often well represented, with *Dicranum scoparium* somewhat less regular. Some other species, while not reaching such a high degree of constancy, are also very typical of this heath-type. Most conspicuous of these is *Genista anglica*, only sparingly represented in other heath-types but abundant in some examples of *Calluna—Arcto-*

staphylos heaths, particularly in the glens of the eastern Grampians, such as Glen Esk, Deeside, Speyside, etc. Considering only this portion of the area within which *Calluna—Arctostaphylos* heaths occur, the constancy of *Genista anglica* is high, and this applies equally to the moss *Dicranum spurium* which, in examples such as Dinnet Moor, is very abundant and, at least in Scotland, of apparently high fidelity to this type of community. Certain additional species are also characteristic when associated in this community-type, although each ranges widely into other communities and none is invariably present. Examples, many of them indicative of a soil base-status approaching that of the herb-rich variants of other types, include *Antennaria dioica*, *Anthoxanthum odoratum*, *Carex pilulifera*, *Campanula rotundifolia*, *Hypericum pulchrum*, *Listera cordata*, *Solidago virgaurea*, *Succisa pratensis*, *Veronica officinalis* and *Viola riviniana* (Table 27, col. 6).

The physiognomy of the community is usually characterised by a patchy canopy of *Calluna*, many of the gaps being occupied by a mat of *Arctostaphylos*. As old bushes of *Calluna* open up in the centre or die out, *Arctostaphylos* creeps into the new gaps, often spreading some distance from its original anchorage. Twisted, prostrate woody stems of *Arctostaphylos* are everywhere found partially buried under new growth of *Calluna*. Patches of bare ground are also frequent, occupied by a rich lichen flora in which the species concerned vary considerably from stand to stand, the more regular perhaps being *Cladonia sylvatica*, *C. impexa* and *C. pyxidata* var. *chlorophaea* (= *C.* "*chlo rophala*").

Altitudinal and edaphic range. Calluna—Arctostaphylos heaths of this type are perhaps more limited altitudinally than the other types described, occurring mainly between the limits of 225 m. and 600 m. They are well represented in the east central Highlands of Scotland, figuring in the survey by McVean and Ratcliffe (1962) and also in Chapter 11 (p. 484). The substratum is often a shallow, well-drained and rather stony soil ("hard ground") of a podsolic type, but with little accumulation of raw humus ($\mathbf{A_0}$) and sometimes with indistinct profile development. Parent materials are perhaps of rather higher base status than those leading, for example, to the deep podsols of the *Calluna—Vaccinium* heaths, but some examples, e.g. Glen Dye on sandy morainic material, are clearly differentiated iron-humus podsols with thick deposition layers of iron and humus in the **B** horizon showing downwardly directed "tongues". In Glen Tanar (Whittaker, 1960) similar communities occur on oligotrophic braunerde, and at Dinnet an excellent example is found on a semi-podsol which was probably under cultivation about 1870. Here there is only a very thin, 6 mm. ($\frac{1}{4}$ in.) accumulation of raw humus, having a pH of 5·0, and the upper 23 cm. (9 in.) of soil, corresponding approximately to plough depth, consist of a more or less uniform admixture of organic and mineral material, grey-brown in colour, about 80 per cent. base-saturated and with abundant burrowing earthworms (Boggie, 1956).

Distribution. The distribution of this heath type (Fig. 42) includes the counties of Angus (Glen Esk), Kincardine (Glen Dye), Aberdeen (Deeside—including GlenTanar Dinnet, Pannanich, etc.), Inverness (Glen Banchor, Allt Mor, Glen Mauckie, Dalwhinnie, Daviot) and Perthshire (Blair Atholl, Keltney Burn).

Relationship to other communities. An account of this heath-type is given by McVean

and Ratcliffe (1962) under the title "Arctostaphyleto—Callunetum". On the whole, it is rather clearly distinct from others in Scotland, with the exception perhaps of the *Calluna—Erica cinerea* communities of the less oceanic character. As mentioned in connection with these (p. 258) some apparently transitional examples containing *Arctostaphylos* occur.

Rather strangely, this community-type seems also to bear only slight relationship to Scandinavian heaths containing *Arctostaphylos*. In western Norway, as in the very north of Scotland, *Arctostaphylos* occurs in the highly oceanic *Calluna—Erica cinerea* heaths, and it is these communities which show greatest floristic affinity with those discussed in this section. Communities from S.W. Sweden containing *Arctostaphylos* are much more akin to the *Calluna—Vaccinium* type and may contain more continental species such as *Genista pilosa* and *Arnica montana*; those in Denmark are generally rich

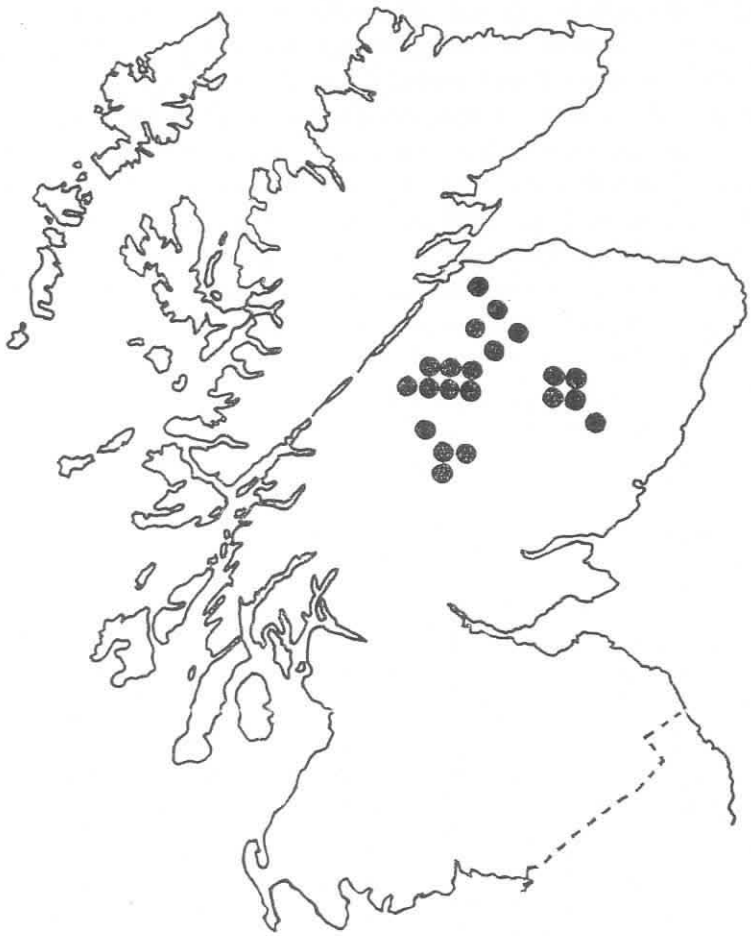


FIG. 42 Distribution of *Calluna-Arctostaphylos* heaths with *Erica cinerea*, *Genista anglica*, *Pyrola media*, *Lathyrus montanus*, etc. (After McVean and Ratcliffe, 1962.)

in *Empetrum nigrum* and although usually including *Genista anglica* show few of the other species here associated with *Arctostaphylos*, linking more closely with next group to be described.

***Calluna—Empetrum nigrum* communities of dry habitats.** Communities in which *Calluna* and *Empetrum nigrum* are the chief species on dry freely drained soils such as blown sand although widespread, for example, in Denmark, are extremely restricted in Scotland. They are confined to old fixed, maritime sand dunes where the sand is siliceous with a low lime-content, in a few places on the north-east and north-west coasts. *Empetrum nigrum* is vigorous and abundant, extending continuously among the *Calluna* or colonising open sites and spreading in big circular patches derived from a single individual. *Erica cinerea* is often present, but *Vaccinium* spp. are lacking. Other flowering plants of high constancy are those of dune heaths in general such as *Ammophila arenaria*, *Carex arenaria*, *Festuca rubra* (or *F. ovina*), *Galium verum* and the moss *Rhytidiadelphus triquetrus*. Otherwise, the only characteristic features of the community-type are its richness in lichen species, again variable from stand to stand but with *Cladonia impexa*, *C. sylvatica* and *Cetraria aculeata* perhaps among the most typical. Chief among the mosses is *Hylocomium splendens*, but *Pleurozium schreberi*, *Hypnum cupressiforme* and *Dicranum scoparium* are also constants. As with other maritime sands, species indicative of at least moderate base-status occur with some frequency, such as *Holcus lanatus*, *Campanula rotundifolia*, *Anthoxanthum odoratum*, *Thymus drucei*, *Lotus corniculatus*, *Viola riviniana* and *Luzula campestris* (Table 27, col. 7).

A variant is:

(*a*) Empetrum-*lichen communities lacking* Calluna. In parts of the habitats occupied by the dry *Calluna-Empetrum* communities there are stands in which *Calluna* is lacking altogether and a version dominated by *Empetrum nigrum* results (Plate 43). This is rich in lichen species, especially *Cladonia sylvatica*, *Cetraria aculeata* and *Cladonia furcata*, but contains few other components apart from *Teesdalia nudicaulis* and a small group of mosses, including *Ceratodon purpureus*, *Polytrichum piliferum* and, where sand deposition occurs, *Rhacomitrium canescens*. Landsberg (1955) suggests that this type of community is in fact seral, developing in areas which, although generally stable, are locally subject to sand erosion or deposition. This accords with the pioneer role of *Empetrum* on some dune heaths on the coasts of Sweden and Denmark, and the stabilising effect of prostrate colonies of *Empetrum* may lead to an increase in the proportion of *Calluna* and the formation of a closed dune heath community.

Altitudinal and edaphic range. In the form described, this community type occurs only within about 30 m. (100 ft.) of sea-level and only on well-drained, stabilised sand at a pH of 4·8-6·0. It occurs where sand has blown over slopes near to the sea, on old fixed dune ridges, and on the irregular hummocky dunes representing the trailing "arms" of an eroded U-shaped dune. The soil profiles may show varying degrees of podsolisation.

Photo A. Tewnian

PLATE 37. Heathland scenery in N.E. Scotland. On hills in distance *Calluna—Vaccinium* heath, in foreground *Calluna—Erica tetralix* heath on soils of impeded drainage.

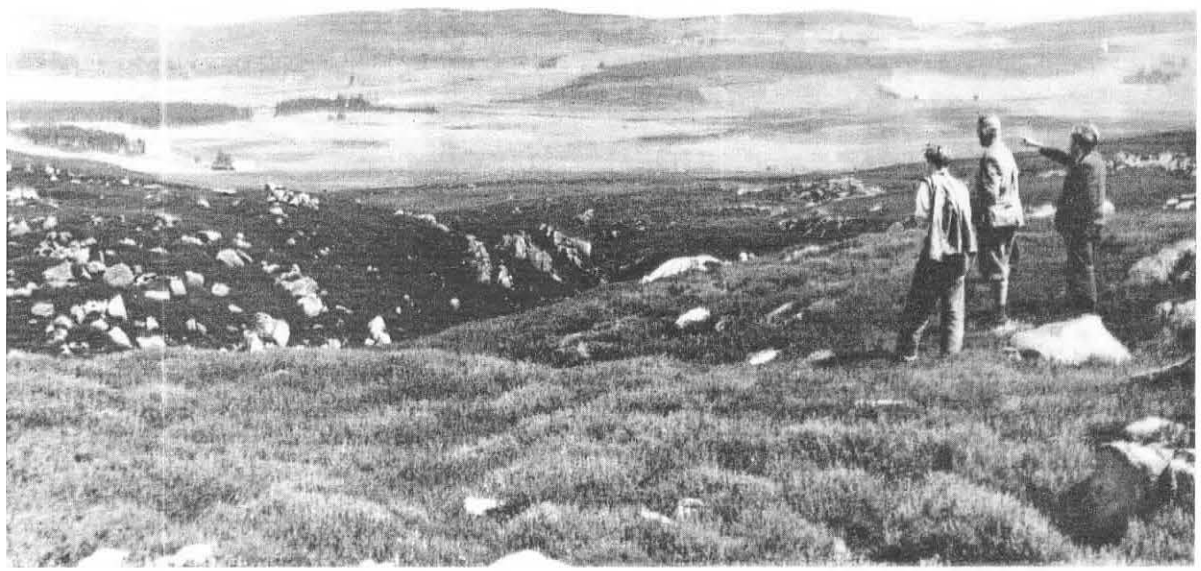
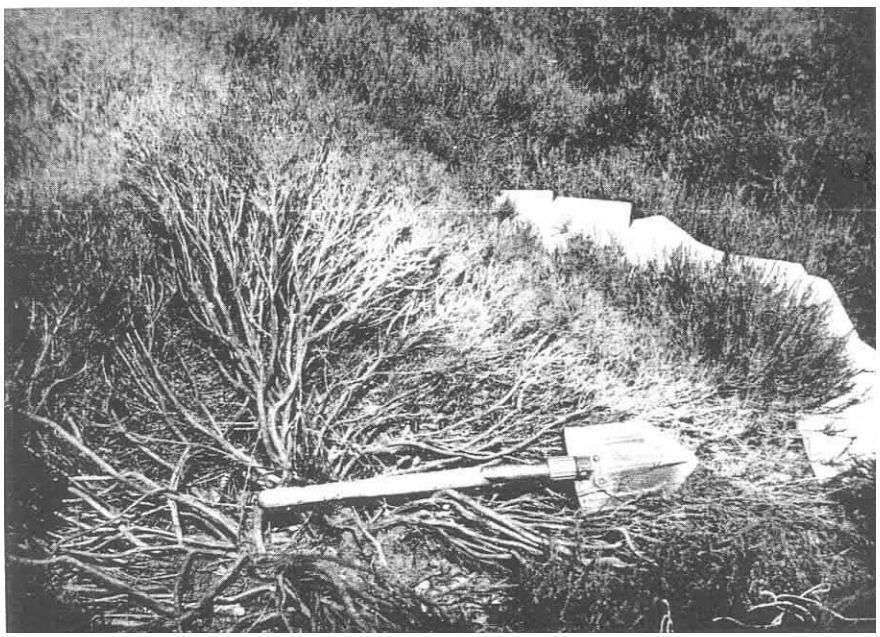


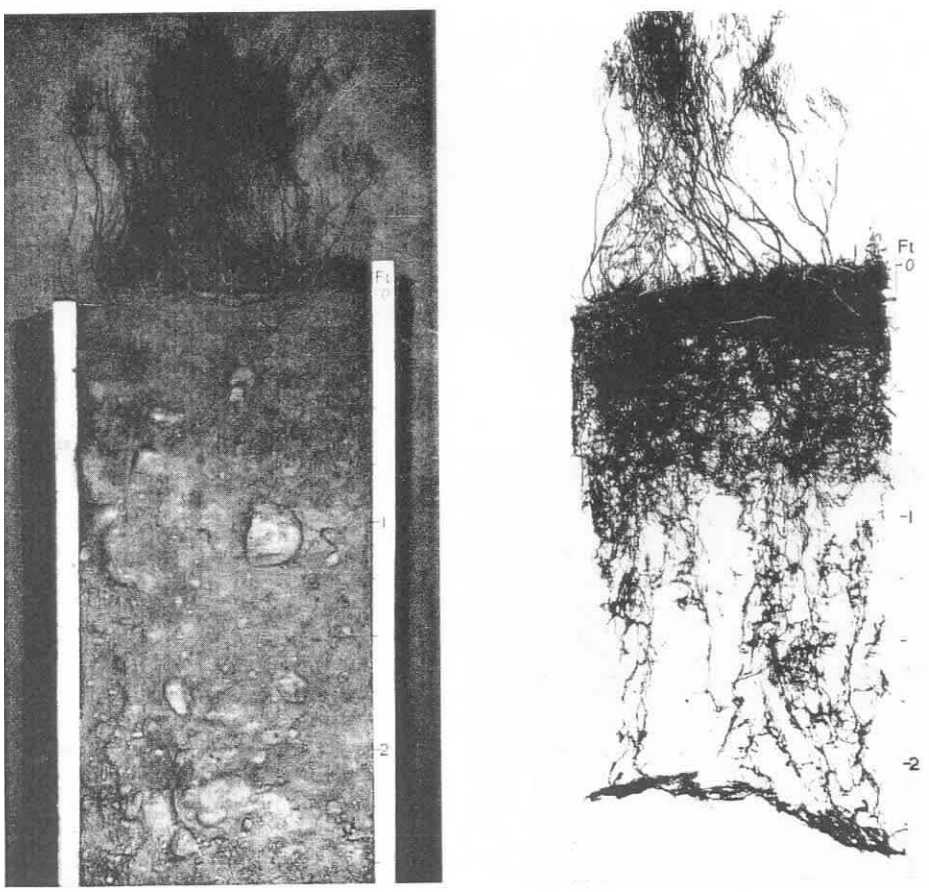
Photo D. Jenkins

PLATE 38. Heathland scenery in N.E. Scotland, near Banchory, Aberdeenshire. Foreground: *Calluna—Arctostaphylos uva-ursi* heath on shallow soil with thin organic "top". Many boulders at surface.

PLATE 39. Dome-shaped form of a mature bush of *Calluna vulgaris* growing without direct competition from neighbouring individuals (top of rule is 1 m. from ground surface).

PLATE 40. Degenerate bush of *Calluna vulgaris* showing central gap caused by death of oldest frame-branches and outward collapse of others. Peripheral branches are still producing green shoots and flowers.





Photos I. Moir

(A) (B)

PLATE 41. (A) Soil profile, and (B) distribution of *Calluna* roots in heath at Dinnet, Aberdeenshire. Note dense aggregation of roots just below soil surface, some extending to lower horizons and spreading out just above the iron-pan. Samples prepared by R. Boggie.

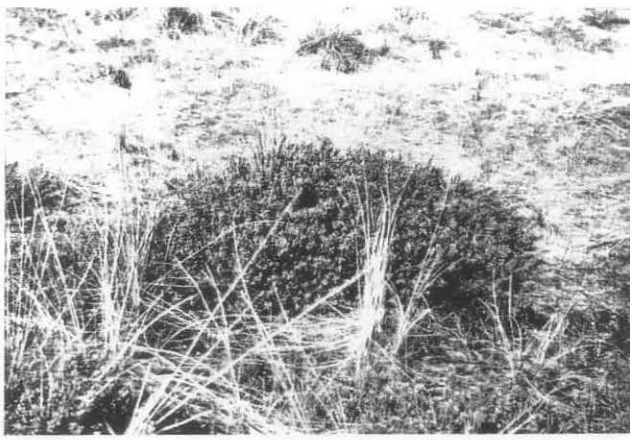


PLATE 42

Entry of a bush of *Erica cinerea* among *Ammophila arenaria*, etc. on a dune system at the Bay of Luce, Wigtownshire.

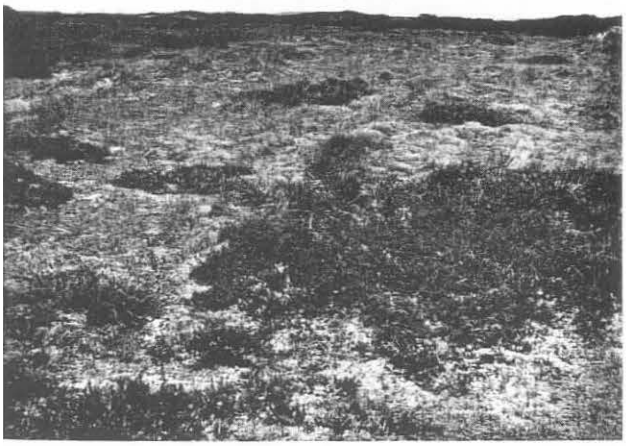


PLATE 43

Empetrum nigrum—lichen community on old stabilized dunes near Collieston, Aberdeenshire (Sands of Forvie).

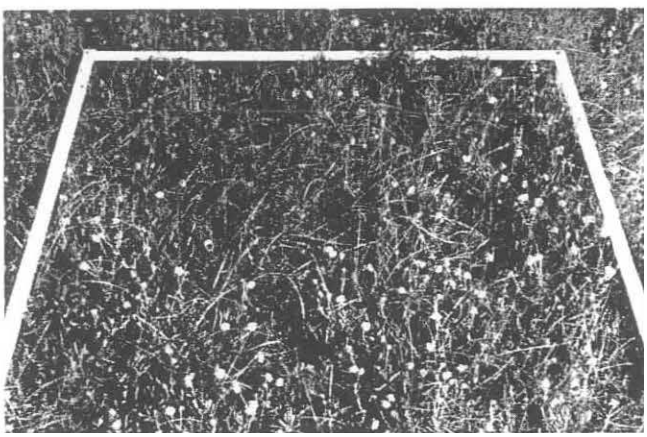


PLATE 44

Calluna—Erica tetralix wet heath, with *Empetrum nigrum* and foliage of *Eriophorum angustifolium*. Near Aberdeen.

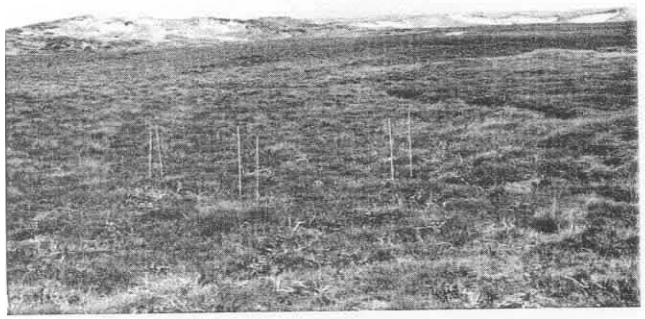


PLATE 45

Dune heath at Sands of Forvie, Aberdeenshire. *Calluna vulgaris* in building phase after burning a degenerating stand (old charred stems still visible). Windward eroded slopes of U-shaped ground.

Photo E. M. Birse

PLATE 46

Pattern of regenerating *Calluna* stands of various ages after burning in strips. Foreground: a peat-hag, and hollow eroded down to parent material. Glen Dye, Aberdeenshire: Clach-na-Ben in distance.

PLATE 47

Mosaic of stands of differing age produced by rotational burning—Geallaig Hill, Crathie, Aberdeenshire. The pattern is emphasized by snow lying on the ground on the sites of recent fires.

Photo D. Jenkins

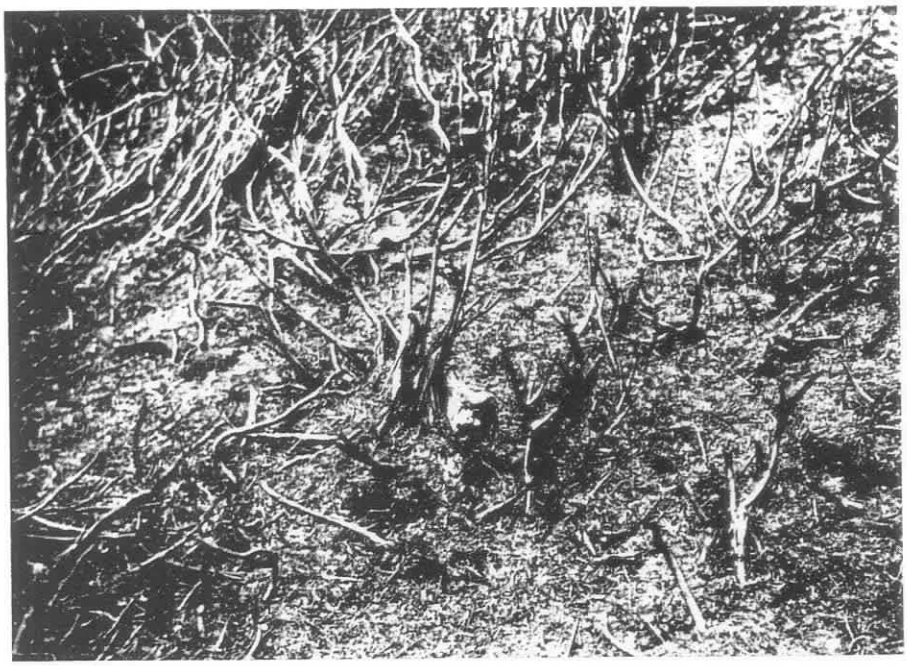
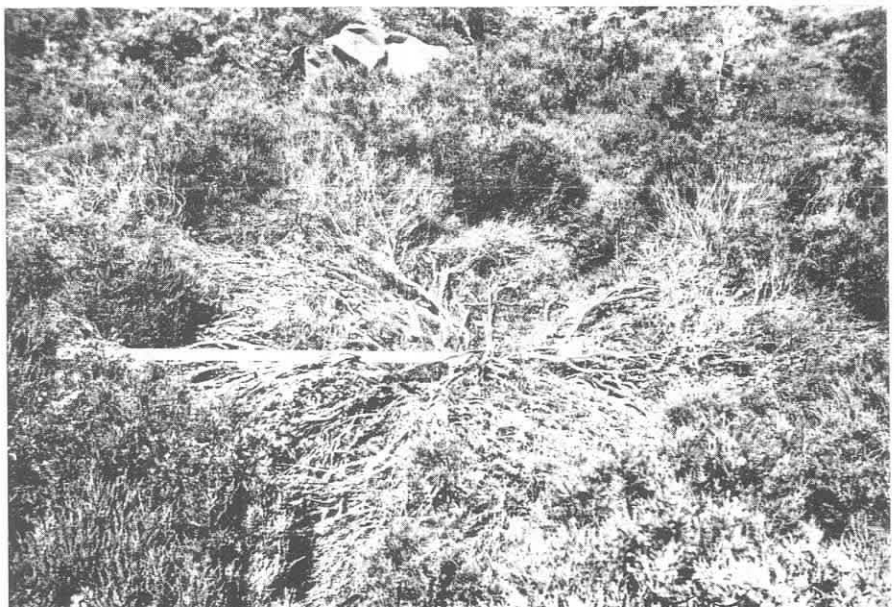


PLATE 48. Charred stems of old *Calluna* plants after burning. Such plants fail to regenerate vegetatively, and reconstitution of vegetational cover, mainly by seedling establishment, is slow.

Photo E. Cormack

PLATE 49. Cyclical change in a *Calluna—Vaccinium vitis-idaea* community. A gap phase has formed in an old *Calluna* bush, the dead stems being colonized by *Hypogymnia physodes*. The ground is occupied by mosses (*Hypnum cupressiforme*, *Pleurozium schreberi*, etc.) and *Vaccinium vitis-idaea* is spreading into the gap. The rule measures 1 m.



Distribution. Well developed on parts of the Aberdeenshire coast, especially at the sands of Forvie (Landsberg, 1955), and smaller patches in Kincardineshire. Also in places on the coast of Wester Ross and perhaps elsewhere.

Relationship to other communities. This type of heath community, occupying a rather distinctive habitat, shows few links with other Scottish types. Apart from the prominence of *Empetrum nigrum* there is little similarity with the type of wet heath in which *Empetrum* also plays an important part (below). Both floristically and ecologically these two *Empetrum*-rich community-types are widely separated, while under conditions somewhat intermediate between them, the role of *Empetrum* is reduced, e.g. in the *Calluna—Vaccinium* communities. This constitutes an ecological problem which is at present under investigation.

Communities showing the closest relationship to those grouped in this section occur in Denmark, especially Jutland (Bøcher, 1943). As in Scotland, they contain very few species of phanerogams apart from those associated with a substratum of blown sand, and are usually rich in lichens, especially *Cladonia sylvatica*, *C. impexa* and *C. "chlorophaea"*. Apart from the scarcity or absence of *Hylocomium splendens*, the bryophytic component is also closely similar. Related communities occur on dunes on the coasts of S.W. Sweden, and in inland localities in N. Germany, N.E. Holland, etc. (Gimingham, 1961).

Heaths on soils of impeded drainage or rather deep organic "top"

Calluna—Erica tetralix* heaths rich in *Empetrum nigrum (Table 26, p. 284, col. 1). Where peaty humus builds up above a gleyed podsolic profile or on deeper peat, *Calluna—Erica tetralix* communities are frequent, and those of the less extremely wet substrata may include *E. nigrum* as a constant component (Plate 44). Beneath the dwarf shrubs, the bryophytic stratum is dominated by *Sphagnum* spp. Most of the species with high constancy-values are characteristic of wet habitats: *Eriophorum vaginatum*, *Juncus squarrosus*, *Polytrichum commune*, *Aulacomnium palustre*, and with slightly lower constancy, *Narthecium ossifragum*, *Eriophorum angustifolium* and *Trichophorum cespitosum*; the last tending to be more abundant in stands with *E. vaginatum* scarce or absent. *Drosera rotundifolia* is frequently present.

The occasional occurrence of species typical of the drier heath-types suggests that the floristic differences are not as great as they might appear, and good evidence for relationship is provided by the high constancy of *Pleurozium schreberi* and *Hypnum cupressiforme*—the former usually contributing appreciable cover. On the west of Scotland and on higher ground, *Vaccinium myrtillus* and *Hylocomium splendens* may also be present.

A variant is:

(*a*) In the extreme north of Scotland, similar habitats may exhibit communities of *Erica tetralix* and *Empetrum nigrum*, lacking *Calluna* but similar in other respects to those described above.

Altitudinal and edaphic range. From little more than sea-level (e.g. behind or between dune ridges where erosion down to the water table has taken place) to about 500 m. in the hills. Mainly on *Sphagnum* peat or related peats and peaty humus.

Distribution. Widespread through the northern part of the country in suitable habitats.

Relationship to other communities. As mentioned above, links are discernible between this type of community and the *Calluna—Vaccinium* heaths, and no doubt the two groups represent different portions of a direction of variation following a gradient in soil moisture regime. Very similar stands occur in S.W. Sweden, Denmark and N.E. Holland, the chief difference being the apparently much reduced role of *Sphagnum* and the frequent occurrence of *Vaccinium uliginosum*. Many of these examples are very rich in species of hepatics.

***Calluna—Erica tetralix* wet heaths.** This important complex of related communities occurs widely where drainage conditions maintain more or less permanently saturated conditions at the surface of an acid soil or peat, although not such as to lead to active peat-building. Such communities may occupy small hollows, or large shallow basins where drainage water collects, or breaks in the slope of a hill where seepage water comes to the surface. Alternatively they may form a zone, sometimes wide and sometimes narrow, towards the foot of a hill slope between the drier heath community above and true bog or "poor fen" below. This zonation may be seen in miniature in dune slacks on the more acid dune systems where the drier *Calluna* with *Ammophila* and *Carex arenaria* is separated by a very narrow zone of *Calluna* with *Erica tetralix* from the floor of the slack, which is frequently dominated by *Salix repens*. Apart from *Calluna* and *Erica tetralix*, the important species tend to be those ranging also into various types of bog community (Chapter 10) such as *Trichophorum cespitosum* and *Narthecium ossifragum*. In a number of the stands *Molinia caerulea* is a prominent component and in some examples, although not all, it is best represented where *Trichophorum* is weakest. *Eriophorum vaginatum*, *E. angustifolium*, *Juncus squarrosus* and *Carex panicea* also have high cover values in certain stands but are absent from others. Insufficient work has been done to establish the reasons for these variations, or the relationships between stands in which these species are differently grouped. *Pleurozium schreberi* and *Hypnum cupressiforme* remain the most constant mosses, *Sphagnum* is usually important and frequently associated are *Aulacomnium palustre*, *Leucobryum glaucum*, *Rhytidiadelphus squarrosus*, *Polytrichum commune* and *Dicranum scoparium*. Hepatics are usually represented, sometimes in considerable abundance and diversity.

Variants include:

On the basis of the occurrence of the associated species characteristic of wet oligotrophic habitats, the following subdivisions may be suggested, although it is sometimes difficult to distinguish between them:

(α) *Rich in* Trichophorum cespitosum (Table 26, col. 2).

(β) *Rich in* Molinia caerulea (Table 26, col. 3).

(γ) Calluna—Erica tetralix *communities with neither of the above species prominent* (Table 26, col. 4).

(δ) Erica tetralix *dominant with* Calluna *sparse or absent.*

(ϵ) *Herb-rich variants* on slightly flushed peats or other soils; these include many of the species also characterising herb-rich variations of other heath-types.

Altitudinal and Edaphic range. Mainly a lowland complex of communities, from sea-level to about 550 m., over gleyed podsolic profiles, shallow wet peat and skeletal soils kept moist by seepage or run-off.

Distribution. Throughout Scotland.

Relationship to other communities. Related wet heaths are common in the sector of N.W. Europe running from Holland through N. Germany to Denmark and the western half of S. Sweden. Similar types occur throughout much of England, but are replaced in S. England and N. France by communities characterised by a number of highly oceanic species. The variants (α) and (β) above are similar to groups of stands entitled "Trichophoreto—Callunetum" and "Molinieto—Callunetum" by McVean and Ratcliffe (1962).

Species which constitute the *Calluna—Erica tetralix* communities also play a part in the mosaic of the hummock-hollow complex of acid bogs, occupying the sides and tops of the hummocks (cf. pp. 450; 460).

***Calluna—Eriophorum vaginatum* wet-heath** (Table 26, col. 5). A community type of rather distinctive physiognomy, consisting of tussocks of *E. vaginatum* interspersed among bushes of *Calluna*, is characteristic of hill peat in parts of Scotland. It ranges from about 150 m. to quite high altitudes (see Chapter 11), taking on a slightly different character above about 600 m. by the addition of montane species such as *Rubus chamaemorus* ("Calluneto-Eriphoretum", McVean and Ratcliffe, 1962). Few analyses from lowland examples are available, but apart from the species mentioned, *Polytrichum commune* is highly constant, often forming dense cushions, and *Sphagnum* spp. also constitute an important component. Areas of acid bog may pass into this community after modification by drainage, and in places it represents an ecotone between a loch-side zone of *E. vaginatum* and drier heaths above. Bog peat dominated by *E. vaginatum* (as at Cruden Moss, Aberdeenshire) may, if the surface begins to dry, be colonised by *Calluna*, the young plants appearing between the tussocks of *Eriophorum*, thus giving rise to *Calluna—Eriophorum* wet heath.

Where *Calluna—Eriophorum vaginatum* communities develop, the water table is frequently to be seen at the surface in the hollows between tussocks from November to February, although the upper horizons may dry out considerably in summer. The pH lies normally between 3·6 and 3·8, and base-saturation is generally less than 30 per cent.

Dynamic Aspects

The origins of heaths—maintenance and reversion

The authors of earlier accounts of British heathlands tended to expect them to constitute a vegetation-type, the chief units of which would conform in status and

developmental history. Thus Tansley (1949), for example, regarded heaths of exposed coastal and high mountain habitats as climatic climaxes, while the remainder, occurring in regions having forest as their theoretical climax vegetation, had to be fitted into his framework as "sub-climaxes", arrested at a particular stage of seral development by edaphic, biotic or anthropogenic factors. While fully aware of the evidence that many examples of heathland had been derived in the past from forest, as clearly indicated in 1911 in *Types of British Vegetation*, he finally concluded (1949) that the heath formation could only be summarised as representing a seral stage in the development of climax woodland on acid soils. This view may be criticised on the ground that the interpretation has been forced to fit the theoretical framework, but recent work has shown that it is rather the attempt to summarise the status of heathlands in a simple manner which is misplaced. Research on the vegetational history of Scotland has shown that here, as elsewhere, heathlands have had numerous different types of origin, and that numerous different factors may be concerned in various combinations in their production. Some heaths, such as those of mountain and coast, may, as Tansley suggested, arise in the course of plant successions. Even here it is often difficult to obtain objective evidence of the unaided replacement of earlier seral stages by heath communities and the question as to whether the latter are themselves seral or climax is equally difficult to settle. For the rest, the ecological history of each area requires independent investigation. In many cases derivation from forest is indicated, but whether this has followed either more or less "natural" changes in climate or soil, or has resulted from the clearance of forest by man, remains a matter for debate. Still other heaths occupy areas formerly grassland or peat bog. These different types of origin will be briefly examined in turn.

Origin in the course of plant succession. It has always been assumed that dune heaths arise in the course of the prisere on blown sand, if conditions of pH, calcium content, etc., become suitable (Plate 45). Transects passing inland across a simple non-calcareous system frequently demonstrate the location of dune heath in dry hollows or flat areas between ridges which have passed through the stage of surface fixation, or on the older stabilised ridges themselves where pH at the surface has fallen to about 6·5 or less. The difficulty confronting this simple explanation is to find evidence of invasion by the heath plants. Detailed examination of the transition zones between fixed dune communities and dune heath on four Aberdeenshire dune systems failed to yield any seedlings or young plants. These zones contain scattered bushes of *Calluna* and *Erica cinerea*, but all were well established or old plants, often compact and dome-shaped and sometimes, in the case of *Calluna*, degenerating (Ritchie, 1951). Such cases suggest a regression rather than an advance of dune heath, and there is evidence that this may be a result of intensive grazing by rabbits which are responsible for the dense, hemi-spherical form of the bushes.

Nevertheless, even if colonisation by heath plants is spasmodic and confined to infrequent periods of relief from rabbit grazing, it is still a seral development and evidence should be forthcoming for this. Such evidence may be found, for example, in the presence of large numbers of dead *Carex arenaria* rhizomes in the sand beneath certain dune heaths in which the species is no longer present (Boggie, 1956), and in the

frequent occurrence of degenerating clumps of *Ammophila arenaria* amongst the heather. Further, the entry of a single plant of *Calluna* into the dune pasture community at St. Cyrus, Kincardineshire, can be dated with certainty to the period 1952-53, a time when the rabbit population was reduced by myxomatosis. This at present is still the only individual in the area, but since the soil pH is not more than 6·2 and calcium carbonate content is below 1·5 per cent. (in spite of some base-enrichment from weathering lavas of nearby cliffs), it may be expected to spread unless prevented by renewed grazing or other factors. The lack of dune heath behind so many Scottish non-calcareous dune systems may perhaps be ascribed, to some extent, to the influence of grazing animals.

Little can be said with certainty about the further seral development of dune heaths, once established. Low shrubs such as *Ulex europaeus* sometimes enter but are seldom important. *Juniperus communis* occurs in examples of dune heaths from Tain on the Dornoch Firth northwards. Species of *Salix* occur in the wetter situations, and occasional seedlings of *Sorbus aucuparia* and *Betula* spp. may be found. It is reasonable to suppose that some type of woodland would eventually develop, at least in the more sheltered situations, if protected from burning and grazing.

Origin from forest. Pollen analyses of peat deposits in various parts of Scotland carried out by Durno (1956, 1957, 1958, 1959) often show an increase in ericoid pollen following upon the transition from Boreal to Atlantic times. This, accompanied by a reduction in total tree pollen, is evidence for some degree of replacement of forest by heath as a result of climatic change before the influence of man was felt (Fig. 43). Generally, however, such heath was transitory and followed by a return of forest. More striking expansions of heath are indicated in Neolithic and Iron Age times from about 2500 B.C., leading eventually to lasting replacement of forest by heath, particularly from the Iron Age (c. 500 B.C.) onwards. This increase first appears in coastal examples and only later in more inland sites where, in many cases, it is confined to a relatively "modern" period. Taking into consideration abundant additional evidence of the increasing activity of man during these times, it is difficult to avoid the conclusion that he played a large part in initiating and continuing the change. Men of late Neolithic cultures, followed by those of the Bronze Age, made their first settlements in coastal areas, where forest clearance would have started. Later this would have extended into more inland districts, to reach its climax in relatively recent times. At the same time, in the sub-atlantic period climatic conditions became rather more favourable for heath vegetation and less so for forest, and it remains impossible to judge the relative contributions of the two linked causes, climate and man, of the origin of many heaths from former forest.

That many heaths indeed occupy former forest sites is shown by the presence of fragments, or stumps, of trees preserved in peaty deposits beneath present-day heath vegetation, even to quite high altitudes (cf. Pearsall, 1950). Since the main dominants (e.g. *Calluna vulgaris*, *Vaccinium* spp.) and several of the other heath species are normally already present under the tree canopy, the extent of vegetational change is not great and examples may be followed on the sites of recently felled woodland. At first the cover of *Calluna* is often less than 50 per cent. and dominance may be shared with *Vaccinium*

myrtillus and one or more grasses, often *Deschampsia flexuosa* which may contribute up to 80 per cent. cover at ground level. In the first few years after felling, the community is distinctly patchy reflecting the irregularities in the former tree canopy. Release from dominance by trees leads to the spread of such species as *Chamaenerion angustifolium*, *Agrostis* spp., *Carex pilulifera*, *Galium saxatile* and *Rumex acetosella*. Some others characteristic of the woodland community such as *Dryopteris dilatata* retain their place.

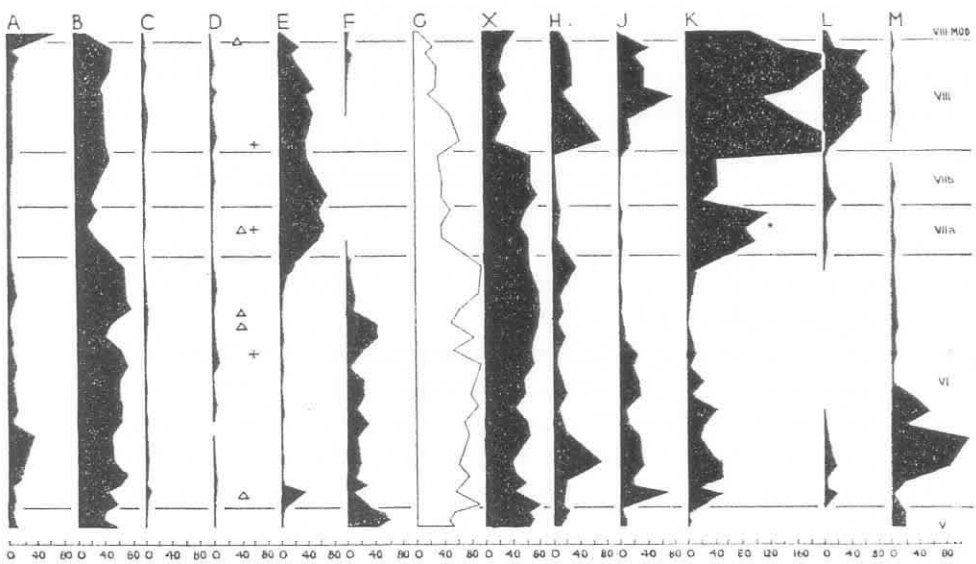


FIG. 43 Pollen diagram from St. Fergus Moss, Aberdeenshire. (S.E. Durno (1956), *Scot. geogr. Mag.*, **72**, 180.) Note temporary rise of Ericoid pollen in Zone VIIa, and marked lasting increase in VIII.

Arboreal species: A. pine (*Pinus*): B. birch (*Betula*): C. oak (*Quercus*): D. elm (*Ulmus*): E. alder (*Alnus*): F. willow (*Salix*): G. hazel (*Corylus*).
Non-arboreal species: H. grass (Gramineae): J. sedges (Cyperaceae): K. heaths (Ericaceae): L. bog moss (Sphagnales): M. ferns (Filicales).
X. Total tree pollen expressed as a percentage of total pollen.
△—ash (*Fraxinus*): +—lime (*Tilia*).
Horizontal lines represent the limits of the pollen zones vi-viii.

Within about five years, however, the expanding bushes of *Calluna* begin to coalesce and the community composition approximates to the heath-type typical of the habitat concerned, with the slow entry of species such as *Erica cinerea* which may have been absent from the original woodland.

Reversion from heath to woodland. Heaths which have replaced destroyed forest are seldom stable communities, except in very exposed habitats or perhaps where long-established on poor soils. In the absence of measures such as burning and grazing, which lead to their perpetuation, they show signs of vegetational change after a time. This first becomes evident in the opening out of the *Calluna* canopy as the plants mature, with subsequent appearance of gaps where the centre of an individual bush has become

degenerate. Space for colonisation by other species is then available, since *Calluna* does not rapidly replace itself on the same spot. Sometimes such spaces are filled by other species of the community (p. 274), but under suitable conditions they provide situations in which tree seedlings will establish and develop when undisturbed by fire and grazing animals. First to appear are usually *Betula* spp. and *Sorbus aucuparia*, but if seed-parents are not too distant *Pinus sylvestris* also colonises. On soils of moderate base status the beginnings of birch scrub may be evident within about ten years of the cessation of burning, and as the tree canopy closes *Calluna* cover diminishes while that of grasses expands. These changes may be slow as *Calluna* persists in shade for a number of years, although failing to regenerate, but in some examples as at Dinnet and Cambus O'May, Aberdeenshire, conversion to birch wood with predominantly grassy ground flora may occur within about twenty years.

Origin from bog. The stratigraphy of the upper horizons of peat beneath present-day heath communities on drained or drying bog sites often gives clear evidence of the relatively recent replacement of *Sphagnum*-dominated communities by *Calluna*. Undoubtedly in many cases this is the result of artificial drainage. Even where there has been no interference with the former bog surface itself, drainage and cultivation of the surrounding countryside may lead to a lowering of the water-table and produce a similar result. Sometimes repeated burning of bog vegetation leads to sufficient drying of the surface for the spread of *Calluna*. Once again, however, it may be that to some extent relatively recent climatic changes have contributed to the change.

Calluna and other wet-heath species constitute a component of the former bog communities, usually occupying the upper parts of hummocks which are often interspersed with pools and channels (cf. Chapter 10). Whenever any part of the bog surface lies above the direct influence of a water-table, for whatever reason, for a considerable period of the year, it becomes open to colonisation by *Calluna*. Wet-heath communities may rapidly develop over former bog, and frequently as drying-out proceeds and *Calluna* becomes increasingly dominant, species of the former communities persist for long periods, in particular *Eriophorum angustifolium* and *E. vaginatum*, both of which root deeply in the wetter peat levels.

Relationship with grassland communities. Fenton (1935, 1949) and others have commented upon the possibility of reversible transitions between heath and grassland communities produced by grazing animals (cf. Chapter 6). On relatively fertile soil, intensive grazing may lead to the replacement of heath by *Agrostis—Festuca* grassland by way of a transitional grass-heath stage. This has been observed in Speyside, Perthshire and elsewhere, and the many instances of abrupt boundaries between heath communities and grassland where a fence divides moorland, lightly grazed by sheep, from the lower-lying, more heavily grazed "in-bye" land of a farm, provide additional evidence (cf. Plates 28 and 29). In other habitats, and especially where rabbit-grazing has a marked effect upon the vegetation, *Deschampsia flexuosa* may become the dominant grass. Abandoned fields sometimes revert to heath, but overgrazing by sheep may permit a more or less permanent replacement of heather by *Pteridium aquilinum* (bracken). On peatlands,

replacement of heath under heavy grazing (often reinforced by burning) by *Nardus stricta* or *Molinia caerulea* is also often virtually irreversible.

Secondary successions following burning

Although the standards of good moorland management are not always observed, they normally demand burning in small strips or patches rather than large areas. A spatial patchwork then results with each patch at a different stage in the recolonisation succession (Plates 46 and 47). Tansley drew attention in 1939 to the lack of any detailed studies of successions following burning on Scottish heaths. As regards the first few months of recolonisation this remains largely true, but it is now possible to summarise certain types of development more fully. Descriptions are given by Fenton (1949) and more detailed studies have been reported by Whittaker (1960). Two main types of sequence may be recognised.

(1) *In which* Calluna *is slow to recover and temporary dominance is attained by other species*

(*a*) On "hard ground".

Calluna—Erica cinerea communities. Where the plants do not exceed 12-15 years of age before burning and the fire is of moderate intensity (temperature around 300°C.), both species begin to regenerate from stem bases during the subsequent year. For about two years the community is mixed, including: *Deschampsia flexuosa*, *Festuca ovina*, *Agrostis* spp. and *Carex pilulifera*, one or more of which may become dominant in small patches; mosses (e.g. *Polytrichum juniperinum*, *P. piliferum*, *Bryum* spp., *Ceratodon purpureus*, *Campylopus* spp.); and, in some instances, a rich selection of *Cladonia* spp. From about the third year onwards the canopy of *Calluna* and *Erica* begins to close up, with *Calluna* re-establishing dominance from about the fifth or sixth year.

If the ericaceous species are killed out, either because of their greater age before burning, or as a result of a more intense fire (e.g. 500-800°C.), their regeneration is entirely from seed (Plate 48). On "hard ground" this is a slow process, particularly in the case of *Calluna*. Sometimes such areas remain largely bare for a number of years, but in more favourable habitats *Deschampsia flexuosa* may exert temporary dominance. Usually, however, within two to five years a dense crop of seedlings is established, in which those of *Erica cinerea* may outnumber *Calluna*. This is followed by a period of dominance by *Erica cinerea* which may last up to five years or more. Repeated observations on fenced plots have shown, however, that the proportion of *Calluna* in the vegetation gradually increases until eventually it exceeds that of *Erica cinerea*.

Calluna—Arctostaphylos uva-ursi communities. By three years after burning, *Arctostaphylos* may be quantitatively the leading species, owing to regeneration from its extensive creeping and partly buried stems. Both *Arctostaphylos* and *Erica cinerea* may exceed *Calluna* in quantity until more than seven years after burning. *Vaccinium* spp., *Antennaria dioica*, *Carex pilulifera* and, to a lesser extent, *Potentilla erecta* also reappear early, developing from undamaged underground vegetative organs, while *Thymus drucei*

and *Veronica officinalis* spread in the open community, particularly after three to five years. Species such as *Genista anglica*, *Pyrola media* and *Listera cordata* may not re-appear until about seven to ten years or more have passed.

(*b*) On "soft ground".

Calluna—Vaccinium communities. Again a temporary phase of dominance by *Deschampsia flexuosa* is often observed, but in many cases it is either followed, or replaced, by a rapid spread of *Vaccinium myrtillus* which, regenerating from rhizomes in the absence of competition with *Calluna*, may become dominant in about three years. *Erica cinerea* is also prominent and *Carex pilulifera* spreads quickly, but most other species of the community, including the majority of bryophytes, do not re-enter until after about four years. From about five years after burning *Calluna* begins to equal and surpass *Vaccinium*.

Communities rich in *Empetrum nigrum*. In a closely similar way, a phase of dominance by *Empetrum nigrum* lasting three to five years or longer may precede the re-establishment of cover by *Calluna*.

Burnt strips of hillsides frequently appear green in contrast to the surrounding brownish colour of *Calluna*, owing to the dominance either of *Vaccinium myrtillus* or *Empetrum nigrum*. However, regeneration of *Calluna*, whether vegetatively or from seed, is quicker and more uniform under the moister conditions provided by "soft ground", and a community not unlike that of the original stand is often established after about four years.

(2) *In which the original community is relatively rapidly reconstituted without intervening stages*

This occurs chiefly under very moist conditions, on peat.

(i) On peaty podsols or drained hill peat, where before burning *Calluna* was dominant with few associates, recolonisation is very largely by *Calluna*. There may be some spread of species such as *Juncus squarrosus*, *Trichophorum cespitosum*, *Nardus stricta* and *Eriophorum vaginatum* which are little damaged by fire, but only under conditions unfavourable for *Calluna* regeneration do any of these become dominant.

(ii) *Calluna—Erica tetralix* communities.

Erica tetralix, regenerating from rhizomes, develops along with *Calluna*, and owing to the wetness of the substratum few of the other species are severely damaged by a well-controlled fire. Thus *Carex panicea*, *Narthecium ossifragum*, *Potentilla erecta*, *Molinia caerulea* and *Trichophorum cespitosum* all produce new growth within the first year, while the outer surfaces of cushions of *Sphagnum* spp. and *Leucobryum glaucum* receive only slight singeing and become green within a few weeks.

The spread of bracken. Under conditions favourable for the regeneration of *Calluna*, burning does not normally lead to the conspicuous spread of *Pteridium aquilinum*. It may,

however, permit the entry of bracken into the community, but the competitive vigour of *Calluna* normally restricts it to a subordinate role or confines it to small patches. From this position it is ready to spread if the *Calluna* is allowed to become degenerate, or if its recolonisation after fire is delayed by heavy grazing, or as a result of excessive frequency of burning.

Cyclical change in heath communities

If individual bushes of heather are allowed to grow undisturbed by grazing or fire, the pioneer and building phases of growth are succeeded at an age of between fifteen and twenty years by a mature phase in which the central branches spread apart, intercepting less light. At an age of about twenty-five years, or more, these branches begin to die and the plant enters a degenerate phase, in which a gap of gradually increasing dimensions

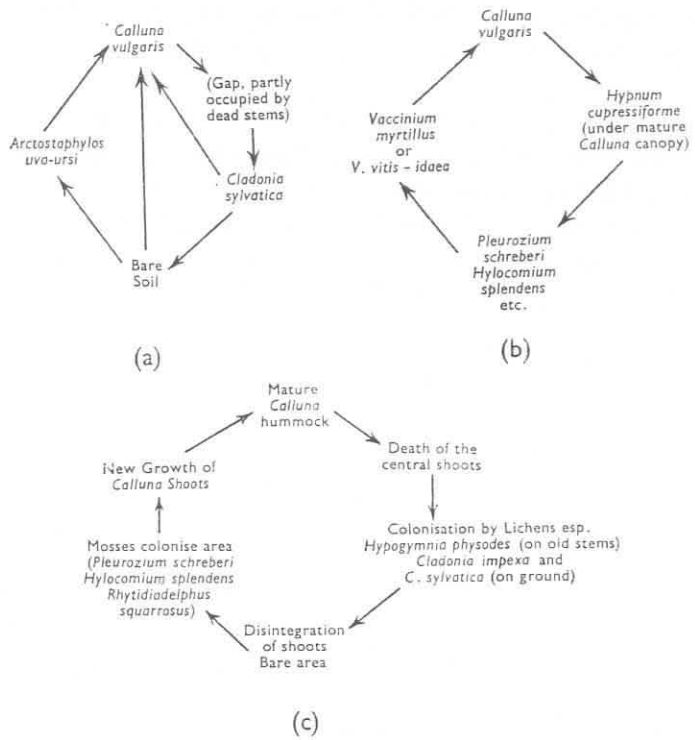


FIG. 44 Examples of cycles of change in heath communities: (a) In *Calluna-Arctostaphylos* communities (after Watt, 1947). (b) In *Calluna-Vaccinium* communities. (c) In dune heath.

develops in the centre of the bush (Plates 40 and 49). Watt (1955) was the first to draw attention to, and name, these phases in the morphological life-history of the plant. Since the bare spaces in the centre of degenerate individuals are more readily invaded by other species than by *Calluna* itself, a cyclical series of changes results in the plant community.

Such a cycle was described by Watt (1947) and Metcalfe (1950) in *Calluna—Arctostaphylos* communities in the Cairngorm region, in which the gap phase is first occupied by *Cladonia sylvatica* anchored on the dead *Calluna* stems. When these disintegrate the *Cladonia* mat is disrupted, and the bare soil becomes covered by *Arctostaphylos uva-ursi* spreading vegetatively from nearby stems. Only later does *Calluna* spread back over the *Arctostaphylos* and replace it when the closed canopy creates dense shade (Fig. 44A).

In *Calluna—Vaccinium* communities similar cycles are observed in which the ground at the centre of the bush becomes occupied, often during the mature phase, by *Hypnum cupressiforme*. As the gap opens out, this is usually largely replaced by more robust mosses such as *Pleurozium schreberi*, *Hylocomium splendens* and *Plagiothecium undulatum*. The bryophyte mat is first penetrated by shoots of *Vaccinium myrtillus* or *V. vitis-idaea* derived from rhizomes, and one of these species may often be seen established in the centre of an old *Calluna* bush which has become ring-shaped in the degenerate phase (Fig. 44B and Plate 49).

Ritchie (1951) has drawn attention to a similar cycle of change in dune heath in which, however, *Calluna* itself recolonises after temporary occupation of the gaps by lichens and mosses (Fig. 44C).

The *Calluna* population in heathland areas which are not regularly burnt and only lightly grazed becomes in time uneven-aged, leading to a markedly patterned community in which other species occupy the gaps formed where plants have become degenerate or dead. Such areas may, for many years, exhibit a mosaic of patches in which different stages of the cycle are represented side by side. The occasional occurrence of a seedling of *Sorbus aucuparia*, *Betula* spp. or *Pinus sylvestris* in the centre of a gap suggests that in the absence of any arresting factor this structure is not stable, but would eventually permit colonisation and replacement by trees. It is, however, virtually impossible in Scotland to find areas in which to test these hypotheses in the presence of good evidence of freedom from grazing and burning for periods of about fifty years.

Utilisation of Heath Lands

At the present time heathlands are maintained over wide areas in Scotland for the purposes of sheep farming and the sport of grouse shooting. To a lesser extent, cattle are grazed on *Calluna* communities in certain parts. Here and there, in the more accessible regions, particularly during the last twenty years, small areas have been converted into pasture or arable land, but the only significant conversion of heathland is in the course of afforestation, which by 1957 had used well over 28,300 ha. (70,000 acres) of heathland (Zehetmeyer, 1960). The rival interests of extensive grazing and afforestation as uses of heathland periodically erupt in controversy over their relative importance and their long-term effects upon soil fertility, while the possibility of substituting some other, radically different form of land use is also raised.

The interests of sheep and grouse are served by basically the same type of moor management, which is designed to maintain much of the heather in its pioneer and

building phases—when productivity of edible green shoots is at a maximum over a large part of a moor. This is achieved by regular burning of strips or patches on rotation such that, as far as possible, each patch is burned at intervals of between eight and about fifteen years, depending upon the habitat and community-type. If regeneration is effective a dense, even-aged stand develops in each patch, and stands of differing age form a large-scale mosaic over the moor. (Older heather is also held to be of value, since it is grazed particularly in winter and may provide keep in critical periods when younger and shorter vegetation is snow-covered. Grouse also require the additional cover it provides. However, it is probable that the majority of moors carry more than enough old heather.)

Treatment by periodic burning, while maintaining a good supply of *Calluna*, leads to impoverishment of the flora and of wild life in general. It has further been claimed that it causes general degradation of soil fertility, as a result of the loss of a certain proportion of the available mineral nutrients, deposited as ash on the soil surface, after each fire. However, insufficient long-term studies have been carried out to provide reliable support for or disproof of this theory. More important, perhaps, is the fact that perpetual monoculture of *Calluna* leads to increasing soil podsolisation and hence reduced availability of nutrients, while the selective grazing habits of sheep, in Scotland virtually the only domestic animal on the moors, are such as to promote the spread of undesirable species including *Pteridium aquilinum* and *Nardus stricta*. Furthermore, the continual cropping of the animal produce from these communities, with negligible provision for the return of substances in the form of fertilisers, inevitably leads in time to habitat deterioration. It is difficult to contrast yields of sheep, cattle, grouse, etc., today with those in past decades or centuries owing to lack of comparability in the available statistics, while veterinary advances and improvements in methods of management might be expected to obscure any decline in yields. None the less, sheep densities of the order of one sheep to between 1·2 and 2·8 ha. (3 and 7 acres) can scarcely be regarded as an efficient form of land use while, merely in terms of productivity, the land devoted to grouse-rearing contributes little and this too appears to be on the decline.

In view of this it is easy to argue that afforestation is more productive, economically more rewarding, and a basically sounder form of land use, since it usually involves a supply of fertiliser to the land and normally, though not always, slowly promotes a return of fertility to the upper layers of the soil. Studies have now been made of the mineral requirements for afforestation of many heath soils, the most appropriate species to plant in the different communities and the most effective methods of planting (Zehetmayr, 1950). Recent research (Leyton, 1954) has thrown some light onto the "check" suffered by Spruce (*Picea abies*) resulting from the effects of competition when planted among *Calluna*. Thus, except in the most exposed localities, there are few areas of lowland heath which cannot be effectively afforested, and there is little doubt that an increase in acreage under forest would be beneficial.

Nevertheless, it is unsound to make direct comparisons between a system which has the resources of a large state enterprise and one which has grown up over the years in the form of relatively small farm units with little capital. Evidence is beginning to

accumulate from various districts of the possibilities of improving heathland for agricultural purposes and, in particular, for carrying increased stocks of sheep and a higher proportion of cattle than at present, without an accompanying deterioration of fertility. There is no reason why investigations on large-scale application of fertilisers and control of grazing in difficult territory should not show the way to replace *Calluna* communities in the better habitats by more valuable pasture, while in poorer districts the quantity and quality of edible material produced by *Calluna* itself could similarly be improved. The hill-sheep industry remains an important part of the agricultural economy of the country, and in this way might be placed on an ecologically sounder foundation. Smaller, more productive areas devoted to sheep-farming would at the same time permit realisation of the equally legitimate claims of forestry for increased scope. In any event, a greater ecological diversity than is at present apparent in the Scottish heathlands would in the long run be of advantage to farmer, forester and ecologist, with little sacrifice of the appeal of the heather moors to the tourist and sportsman.

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TABLE 25

Synoptic Table showing Composition of Community-types in the Euoceanic Heath Series

Figures in these columns show % presence of each species in the stands sampled

	Calluna—Empetrum hermaphroditum communities	*Calluna—Erica cinerea* heaths		
		"Typical" examples	Herb-rich variants	Dune-heath variants
Localities	Islands in Shetland lochs	S. Uist, N. coast of Sutherland, Orkney	S. Uist, Sutherland, Ross-shire, Rhum, Shetland, Orkney, Aberdeenshire	Wigtownshire
No. of stands sampled	6	7	12	2
Sample area	Variable	4 sq. m.	4 sq. m.	4 sq. m.
Altitude range	Up to 150 m.	Up to 90 m.	15–350 m.	Up to 50 m.
Sorbus aucuparia	16	...	8	
Calluna vulgaris	100	100	100	++
Empetrum hermaphroditum	83	14	17	
E. nigrum	...	43	25	
Erica cinerea	16	100	100	++
E. tetralix	...	43	25	
Salix repens	...	29	25	
Vaccinium myrtillus	...	29	8	
V. vitis-idaea	16	...	8	
Blechnum spicant	32	57	50	
Pteridium aquilinum	...	43	25	+
Agrostis canina/A. tenuis	16	86	92	++
Anthoxanthum odoratum	16	43	75	
Deschampsia flexuosa	83	...	25	
Festuca ovina	...	...	58	
F. rubra	...	43	42	+
Molinia caerulea	10	43	42	
Nardus stricta	...	29	33	
Sieglingia decumbens	...	14	58	

Carex binervis . . .	50	57	25	
Carex nigra	16	14	...	
Carex panicea . . .	...	29	58	
Dactylorchis maculata ssp. *ericetorum* . . .	...	29	25	
Luzula campestris . . .	16	...	17	++
L. multiflora	32	29	17	
Trichophorum cespitosum . .	16		17	
Campanula rotundifolia . .	...	29	8	
Euphrasia spp. . . .	32 (*E. scotica*)	...	58	
Galium saxatile . . .	...	14	25	
G. verum	...	29	...	++
Hypericum pulchrum . .	...	71	92	
Linum catharticum . .	...	14	33	
Lotus corniculatus . . .	...	14	50	++
Pedicularis spp. . . .	...	29	17	
Plantago lanceolata . .	...	14	42	
Polygala serpyllifolia . .	...	29	58	
Potentilla erecta . . .	100	86	92	
Rhinanthus minor agg. . .	100	...	17	
Rumex acetosa . . .	32	...	8	
Solidago virgaurea . . .	50	...	17	
Succisa pratensis . . .	16	29	42	
Thymus drucei . . .	...	14	75	+
Trifolium repens . . .	...	14	25	
Veronica officinalis . . .	...	...	8	++
Viola riviniana . . .	...	43	58	++
Breutelia chrysocoma . .	...	14	17	
Dicranum scoparium . .	...	57	42	+
Hylocomium splendens . .	...	71	67	
Hypnum cupressiforme . .	...	86	83	++
Pleurozium schreberi . .	...	29	42	+
Pseudoscleropodium purum .	...	14	58	
Rhacomitrium lanuginosum .	32	14	17	
Rhytidiadelphus loreus . .	...	29	8	
R. squarrosus . . .	...	29	42	
R. triquetrus	...	29	42	+
Thuidium tamariscinum . .	...	14	25	
Diplophyllum albicans . .	...	29	17	

[continued]

	Calluna—Empetrum hermaphroditum communities	*Calluna—Erica cinerea* heaths		
		"Typical" examples	Herb-rich variants	Dune-heath variants
Localities	Islands in Shetland lochs	S. Uist, N. coast of Sutherland, Orkney	S. Uist, Sutherland, Ross-shire, Rhum, Shetland, Orkney, Aberdeenshire	Wigtownshire
No. of stands sampled	6	7	12	2
Sample area	Variable	4 sq. m.	4 sq. m.	4 sq. m.
Altitude range	Up to 150 m.	Up to 90 m.	15–350 m.	Up to 50 m.
C adonia rangiferina	...	29	8	++
C. sylvatica	...	14	17	
Additional species recorded in one only of the community-types included in this table:				Note: ++ = Occurring in both stands. + = Occurring in one stand.
	Juniperus communis ssp. *nana* 16	*Arctostaphylos uva-ursi* 29	*Lonicera periclymenum* 8	*Aira caryophyllea* +
	Vaccinium uliginosum 16	*Agrostis stolonifera* 29	*Rubus fruticosus* agg. 8	*A. praecox* +
	Polypodium vulgare 83	*Campylopus flexuosus* 14	*Athyrium filix-femina* 8	*Ammophila arenaria* ++
	Eriophorum angustifolium 32	*Dicranum majus* 14	*Lycopodium selago* 17	*Carex arenaria* ++
	Luzula sylvatica 32	*Leucobryum glaucum* 14	*Selaginella selaginoides* 17	*Sedum acre* +
		Plagiothecium undulatum 57	*Cynosurus cristatus* 17	*Veronica chamaedrys* +
		Polytrichum commune 14	*Festuca vivipara* 17	*Polytrichum juniperinum* ++
		Cetraria islandica 14	*Holcus lanatus* 8	*Lophocolea bidentata* +
			Koeleria cristata 25	*Ptilidium ciliare* ++
			Carex flacca 8	*Cetraria aculeata* +
			C. pilulifera 50	
			C. pulicaris 42	
			Listera cordata 17	
			Alchemilla alpina 17	
			Anemone nemorosa 17	
			Angelica sylvestris 8	
			Antennaria dioica 58	
			Anthyllis vulneraria 8	
			Armeria maritima 8	
			Cirsium heterophyllum 17	
			Dryas octopetala 8	

			Filipendula ulmaria 8	
			Galium boreale 17	
			Gentianella campestris 8	
			Geum rivale 17	
			Hieracium pilosella 17	
			Hypochoeris radicata 33	
			Lathyrus montanus 25	
			Leontodon autumnalis 17	
			L. hispidus 8	
			Lysimachia nemorum 8	
			Parnassia palustris 8	
			Plantago maritima 33	
			Primula vulgaris 25	
			Prunella vulgaris 25	
			Ranunculus acris 17	
			Taraxacum officinale agg. 8	
			Thalictrum alpinum 17	
			Trifolium pratense 17	
			Trollius europaeus 25	
			Vicia sepium 8	
			Acrocladium cuspidatum 17	
			Ctenidium molluscum 17	
			Drepanocladus uncinatus 8	
			Fissidens osmundoides 17	
			Isothecium myosuroides 17	

Col. 1—Data from Spence (1960).

Col. 3—Includes data from McVean and Ratcliffe (1962).

TABLE 26

Synoptic Table showing Composition of Community-types in Heaths on Soils of Impeded Drainage, etc.

Figures in these columns show % presence of each species in the stands sample

	Calluna—Erica tetralix heaths rich in *Empetrum nigrum*	*Calluna—Erica tetralix* wet heaths			*Calluna—Eriophorum vaginatum* wet heath
		Rich in *Trichophorum cespitosum*	Rich in *Molinia caerulea*	Neither *Trichophorum* nor *Molinia* prominent	
Localities	Orkney, Inverness-shire, Aberdeenshire, Kincardineshire	Wigtownshire, Argyll, W. Ross, Sutherland, Inverness-shire, Moray, Nairn, Aberdeenshire, Kincardineshire, Angus	W. Ross, Inverness-shire, Aberdeenshire, Kincardineshire, Perthshire	Wigtownshire, Sutherland, Aberdeenshire, Kincardineshire, Perthshire	Aberdeenshire, Perthshire
No. of stands sampled	20	30	15	11	3
Sample area	4 sq. m.	4 sq. m.	4 sq. m.	4 sq. m.	Variable
Altitude range	10–500 m.	50–600 m.	50–300 m.	50–300 m.	50–400 m.
Calluna vulgaris	100	100	100	100	100
Empetrum nigrum	100	...	...	9	33
Erica cinerea	10	43	47	18	...
E. tetralix	85	100	93	100	100
Genista anglica	5	10	...	...	...
Myrica gale	...	...	33	9	...
Vaccinium myrtillus	10	13	20	18	...
V. vitis-idaea	5	3	7	...	...
Blechnum spicant	5	...	7	...	...
Agrostis canina/tenuis	15	7	20	27	...
A. stolonifera	15	...	7	9	...
Anthoxanthum odoratum	5	...	7	9	...
Deschampsia cespitosa	...	...	7	9	...
D. flexuosa	10	7	40	46	...
Festuca ovina	10	...	7	9	...
F. rubra	5	...	...	9	...
Molinia caerulea	10	40	100	9	...
Nardus stricta	25	3	33	36	...

Carex arenaria	5	...	...	18	...
C. binervis	15	3	13	9	...
C. echinata	10	3	27	...	...
C. nigra	...	...	7	...	33
C. panicea	20	43	27	...	...
C. pilulifera	...	30	20	...	...
Eriophorum angustifolium	45	30	27	55	100
E. vaginatum	60	27	...	55	100
Juncus effusus	15	...	7	27	...
J. squarrosus	60	30	27	36	...
Listera cordata	5	...	7	...	...
Luzula multiflora	5	3	...	...	...
Narthecium ossifragum	50	67	33	46	33
Trichophorum cespitosum	40	100	67	18	33
Drosera rotundifolia	30	3	7	9	...
Galium saxatile	5	...	7	...	...
Hypericum pulchrum	...	...	7	9	...
Pinguicula vulgaris	5	10	7	9	...
Polygala serpyllifolia	...	3	27	9	...
Potentilla erecta	15	33	93	55	...
Rubus chamaemorus	5	...	...	9	...
Succisa pratensis	5	...	27	18	...
Veronica officinalis	...	...	7	27	...
Viola riviniana	...	...	7	9	...
Aulacomnium palustre	55	3	20	55	67
Breutelia chrysocoma	3	...	13	...	...
Campylopus flexuosus	...	13	13	...	33
Dicranum scoparium	30	33	40	73	100
Hylocomium splendens	20	20	67	36	...
Hypnum cupressiforme	80	70	73	82	100
Leucobryum glaucum	3	23	33	9	...
Mnium hornum	15	...	...	18	...
Plagiothecium undulatum	30	3	33	27	33
Pleurozium schreberi	95	27	67	82	67
Pohlia nutans	15	7	7	46	100
Polytrichum commune	60	13	...	73	33
P. juniperinum	10	3	7	9	100
Rhacomitrium lanuginosum	10	23	27	...	...

[continued]

	Calluna—Erica tetralix heaths rich in *Empetrum nigrum*	*Calluna—Erica tetralix* wet heaths			*Calluna—Eriophorum vaginatum* wet heath
		Rich in *Trichophorum cespitosum*	Rich in *Molinia caerulea*	Neither *Trichophorum* nor *Molinia* prominent	
Localities	Orkney, Inverness-shire, Aberdeenshire, Kincardineshire	Wigtownshire, Argyll, W. Ross, Sutherland, Inverness-shire, Moray, Nairn, Aberdeenshire, Kincardineshire, Angus	W. Ross, Inverness-shire, Aberdeenshire, Kincardineshire, Perthshire	Wigtownshire, Sutherland, Aberdeenshire, Kincardineshire, Perthshire	Aberdeenshire, Perthshire
No. of stands sampled	20	30	15	11	3
Sample area	4 sq. m.	4 sq. m.	4 sq. m.	4 sq. m.	Variable
Altitude range	10–500 m.	50–600 m.	50–300 m.	50–300 m.	50–400 m.
Rhytidiadelphus loreus	15	7	40	9	...
R. squarrosus	10	7	27	37	...
R. triquetrus	5	...	7	18	...
Sphagnum spp.	85	57*	73†	46‡	67
Alicularia scalaris	...	...	7	9	...
Barbilophozia floerkii	5	3	...	...	...
Calypogeia trichomanis	10	3	7	36	...
Diplophyllum albicans	...	3	20	...	...
Gymnocolea inflata	15	...	...	9	...
Lophocolea bidentata	10	7	7	18	33
Lophozia ventricosa	5	7	7	...	33
Mylia anomala	...	...	...	9	33
Odontoschisma sphagni	...	7	27	...	...
Scapania gracilis	...	7	7	9	...
Cladonia "chlorophaea"	5	...	...	...	33
C. coccifera	...	7	20	9	33
C. gracilis	...	10	7	...	33
C. impexa	10	30	20	9	33
C. pyxidata	...	47	33	18	...
C. rangiferina	5	10	...	...	...
C. squamosa	10	3	7	...	33
C. sylvatica	25	17	13	9	33
C. uncialis	...	33	13	...	...

Additional species recorded in one only of the community-types included in the table:	*Empetrum hermaphroditum* 5 *Holcus lanatus* 5 *Luzula campestris* 5 *Chamaenerion angustifolium* 5 *Viola palustris* 5 *Orthodontium lineare* 5 *Pseudoscleropodium purum* 5 *Cephaloziella* sp 5 *Plagiochila asplenioides* 5 *Cladonia fimbriata* 5 *C. pityrea* 5 *Lecanora varia* 5	*Arctostaphylos uva-ursi* 3 *Betula nana* 3 *Juniperus communis* ssp. *nana* 3 *Lycopodium selago* 7 *Carex bigelowii* 3 *Dactylorchis maculata* ssp. *ericetorum* 3 *Juncus kochii* 3 *Antennaria dioica* 3 *Pedicularis sylvatica* 3 *Campylopus atrovirens* 13 *Dicranella heteromalla* 3 *Anastrepta orcadensis* 3 *Leptoscyphus anomalus* 7 *L. taylori* 10 *Pleurozia purpurea* 7 *Cetraria islandica* 3 *C. aculeata* 7	*Salix aurita* 7 *Equisetum sylvaticum* 7 *Festuca vivipara* 7 *Juncus conglomeratus* 7 *Trientalis europaea* 7 *Thuidium tamariscinum* 13 *Cladonia cornuta* 7	*Salix repens* 27 *Carex demissa* 9 *C. pulicaris* 9 *Juncus articulatus* 9 *Lotus corniculatus* 9 *Plantago lanceolata* 9 *Rumex acetosella* 9 *Taraxacum officinale* agg. 9 *Trifolium repens* 9 *Acrocladium cuspidatum* 9 *Ceratodon purpureus* 9 *Dicranella palustris* 9 *Calypogeia fissa* 9 *Lophozia excisa* 9 *L. incisa* 9 *Peltigera* sp. 9	*Cephalozia connivens* 33 *Cladonia furcata* 33

Data from McVean and Ratcliffe (1962) have been incorporated in the above table.

* Species recorded include:
S. capillaceum
S. compactum
S. palustre
S. papillosum
S. plumulosum
S. robustum
S. rubellum
S. tenellum

† Species recorded include:
S. capillaceum
S. compactum
S. palustre
S. papillosum
S. plumulosum
S. robustum
S. rubellum
S. tenellum

‡ Species recorded include:
S. capillaceum
S. palustre
S. papillosum
S. rubellum

	Calluna—Erica cinerea heaths (lacking strong oceanic element)			*Calluna—Vaccinium* heaths		*Calluna—Arctostaphylos* heaths	*Calluna—Empetrum nigrum* heaths of dry soils
	"Typical" examples	Stands dominated by *Calluna* alone	Stands including *Arctostaphylos uva-ursi*	Stands with *V. vitis-idaea*, normally *V. myrtillus* also	Stands with *V. myrtillus* only		
Localities	Wigtownshire, W. Ross, Orkney, Aberdeenshire, Kincardineshire	Wigtownshire, Aberdeenshire, Kincardineshire	Aberdeenshire, Kincardineshire	Caithness, Inverness-shire, Aberdeenshire, Kincardineshire, Perthshire	W. Ross, Sutherland, Caithness, Aberdeenshire, Kincardineshire	Inverness-shire, Aberdeenshire, Kincardineshire Angus, Perthshire	Coast of areas in W. Ross, Aberdeenshire, Kincardineshire
No. of stands sampled	21	5	7	62	28	25	12
Sample area	Variable	4 sq. m.	4 sq. m.	Variable	Variable	4 sq. m.	4 sq. m.
Altitude range	10–500 m.	10–100 m.	250–500 m.	100–600 m.	10–600 m.	225–600 m.	5–30 m.
Juniperus communis	...	...	...	2	...	4	...
Sarothamnus scoparius	5	...	...	...	7	...	...
Sorbus aucuparia	5	...	...	8	14	4	...
Ulex europaeus	5	...	...	3	14	...	...
Arctostaphylos uva-ursi	5	...	100	8	...	100	...
Calluna vulgaris	100	100	100	100	100	100	100
Empetrum hermaphroditum	...	...	...	14	7	8	...
E. nigrum	...	40	14	36	29	4	100
Erica cinerea	100	...	86	44	57	92	42
E. tetralix	33	60	100	32	14	12	25
Genista anglica	10	20	14	5	...	64	...
Vaccinium myrtillus	10	...	14	89	100	24	...
V. vitis-idaea	5	...	...	100	...	60	...
Blechnum spicant	29	...	43	23	11	4	...
Lycopodium annotinum	...	...	...	2	4	...	...
Pteridium aquilinum	10	...	29	8	14	...	...
Agrostis canina/tenuis	38	20	43	14	29	48	75
Ammophila arenaria	...	20	...	...	...	...	75
A. stolonifera	5	...	14	...	...	...	25
Anthoxanthum odoratum	5	...	...	7	...	32	25
Deschampsia flexuosa	33	40	29	61	71	52	17
Festuca ovina	19	20	43	5	29	52	67
F. rubra	...	...	...	2	...	...	17
Molinia caerulea	5	...	14	...	11	...	...
Nardus stricta	...	...	29	8	21	...	...
Sieglingia decumbens	19	...	14	3	11	12	8
Carex binervis	...	60	14	7	7	8	...
C. panicea	29	...	14	7	29	12	...
C. pilulifera	52	20	14	16	14	44	...
Eriophorum angustifolium	...	40	14	3	...	...	17
E. vaginatum	...	...	...	8	...	...	...
Juncus effusus	...	...	...	2	11	...	17
J. squarrosus	24	20	29	21	25	...	25
Luzula campestris/multiflora	10	...	...	10	11	40	42
L. pilosa	5	...	14	2	29	...	8
L. sylvatica	...	...	...	3	7	...	...
Listera cordata	...	40	...	8	14	16	...
Trichophorum cespitosum	52	20	43	24	14	12	...
Achillea millefolium	5	...	...	8	...	20	...
Antennaria dioica	10	...	14	2	7	16	33
Campanula rotundifolia	5	...	...	2	4	...	...
Chamaenerion angustifolium	...	...	...	2	4	...	...
Drosera rotundifolia	...	...	...	...	...	4	...
Euphrasia sp.	5	...	...	18	32	28	25
Galium saxatile	14	20	14	2	...	...	17
Hieracium pilosella	...	...	...	5	7	28	...
Hypericum pulchrum	10	...	...	2	...	44	...
Lathyrus montanus	...	...	...	...	...	48	35
Lotus corniculatus	...	...	...	3	4	...	...
Pedicularis spp.	5	...	...	2	10	28	17
Polygala serpyllifolia	14	...	43	37	57	64	42
Potentilla erecta	43	60	43	...	...	44	...
Pyrola media	...	...	...	11	4	...	...
Rubus chamaemorus	...	...	...	...	...	...	8

	Calluna—Erica cinerea heaths (lacking strong oceanic element)			*Calluna—Vaccinium* heaths		*Calluna—Arctostaphylos* heaths	*Calluna—Em* heaths of
	"Typical" examples	Stands dominated by *Calluna* alone	Stands including *Arctostaphylos uva-ursi*	Stands with *V. vitis-idaea*, normally *V. myrtillus* also	Stands with *V. myrtillus* only		
Localities	Wigtownshire, W. Ross, Orkney, Aberdeenshire, Kincardineshire	Wigtownshire, Aberdeenshire, Kincardineshire	Aberdeenshire, Kincardineshire	Caithness, Inverness-shire, Aberdeenshire, Kincardineshire, Perthshire	W. Ross, Sutherland, Caithness, Aberdeenshire, Kincardineshire	Inverness-shire, Aberdeenshire, Kincardineshire Angus, Perthshire	Coast of area Aberdeenshi Kincardines
No. of stands sampled	21	5	7	62	28	25	1
Sample area	Variable	4 sq. m.	4 sq. m.	Variable	Variable	4 sq. m.	4 sq
Altitude range	10–500 m.	10–100 m.	250–500 m.	100–600 m.	10–600 m.	225–600 m.	5–3
Juniperus communis	...	...	...	2	...	4	.
Sarothamnus scoparius	5	...	...	...	7	...	.
Sorbus aucuparia	5	...	...	8	14	4	.
Ulex europaeus	5	...	...	3	14	...	.
Arctostaphylos uva-ursi	5	...	100	8	...	100	.
Calluna vulgaris	100	100	100	100	100	100	10
Empetrum hermaphroditum	...	...	...	14	7	8	.
E. nigrum	...	40	14	36	29	4	10
Erica cinerea	100	...	86	44	57	92	4
E. tetralix	33	60	100	32	14	12	2
Genista anglica	10	20	14	5	...	64	.
Vaccinium myrtillus	10	...	14	89	100	24	.
V. vitis-idaea	5	...	...	100	...	60	.
Blechnum spicant	29	...	43	23	11	4	.
Lycopodium annotinum	...	...	...	2	4	...	.
Pteridium aquilinum	10	...	29	8	14	...	.
Agrostis canina/tenuis	38	20	43	14	29	48	7
Ammophila arenaria	...	20	...	...	...	...	7
A. stolonifera	5	...	14	...	...	...	2
Anthoxanthum odoratum	5	...	...	7	...	32	2
Deschampsia flexuosa	33	40	29	61	71	52	1
Festuca ovina	19	20	43	5	29	52	6
F. rubra	...	...	...	2	...	...	1
Molinia caerulea	5	...	14	...	11	...	.
Nardus stricta	...	...	29	8	21	...	.
Sieglingia decumbens	19	...	14	3	11	12	
Carex binervis	...	60	14	7	7	8	.
C. panicea	29	...	14	7	29	12	.
C. pilulifera	52	20	14	16	14	44	.
Eriophorum angustifolium	...	40	14	3	...	...	1
E. vaginatum	...	...	...	8	...	...	.
Juncus effusus	...	...	...	2	11	...	1
J. squarrosus	24	20	29	21	25	...	2
Luzula campestris/ multiflora	10	...	...	10	11	40	4
L. pilosa	5	...	14	2	29	...	
L. sylvatica	...	...	...	3	7	...	.
Listera cordata	...	40	...	8	14	16	.
Trichophorum cespitosum	52	20	43	24	14	12	.
Achillea millefolium	5	...	...				
Antennaria dioica	10	...	14	8	...	20	.
Campanula rotundifolia	5	...	...	2	7	16	3
Chamaenerion angustifolium	...	...	...	2	4	...	.

Drosera rotundifolia	...	...	...	2				
Euphrasia sp.	5	...	...	...	...	4	...	
Galium saxatile	14	20	14	18	32	28	25	
Hieracium pilosella	...	...	...	2	...	...	17	
Hypericum pulchrum	10	...	...	5	7	28	...	
Lathyrus montanus	...	...	...	2	...	44	...	
Lotus corniculatus	...	...	...	...	...	48	25	
Pedicularis spp.	5	...	...	3	4	...	...	
Polygala serpyllifolia	14	...	43	2	10	28	17	
Potentilla erecta	43	60	43	37	57	64	42	
Pyrola media	...	...	...	...	...	44	...	
Rubus chamaemorus	...	...	...	11	4	...	...	
Rumex acetosa	5	...	...	...	...	...	8	
Rumex acetosella	5	...	29	2	14	...	42	
Senecio jacobaea	...	...	...	...	...	4	25	
Succisa pratensis	5	...	...	3	7	16	...	
Thymus drucei	...	...	...	...	...	4	17	
Trientalis europaea	...	...	...	10	...	20	..	
Trifolium repens	...	...	...	...	...	...	17	
Veronica officinalis	5	...	...	...	...	20	..	
Viola riviniana	...	...	...	7	4	52	3	
Aulacomnium palustre	5	40	...	8	7	...	..	
Breutelia chrysocoma	10	...	...	...	...	...	..	
Campylopus flexuosus	24	...	14	...	14	...	1	
Ceratodon purpureus	...	...	14	2	21	4	4	
Dicranum majus	...	...	...	5	4	...	..	
D. scoparium	33	60	71	47	71	48	6	
D. spurium	5	...	...	...	...	12	..	
Eurhynchium praelongum	...	20	...	...	4	...	..	
Hylocomium splendens	24	40	29	52	54	44	9	
Hypnum cupressiforme	67	80	86	63	82	60	8	
Leucobryum glaucum	10	...	14	10	14	...	.	
Mnium spp.	5	20	...	5	4	...		
Pleurozium schreberi	33	80	43	63	82	44	9	
Poltia nutans	14	20	43	3	39	8		
Plagiothecium undulatum	24	80	14	23	25	8	1	
Polytrichum commune	14	20	14	39	39	16		
P. juniperinum	14	...	14	5	36	4	2	
P. piliferum	...	20	...	2	...	4		
Pseudoscleropodium purum	...	20	...	7	11	20	1	
Rhacomitrium lanuginosum	...	...	...	7	4	8	.	
Rhytidiadelphus loreus	14	...	...	11	...	20	.	
R. squarrosus	14	20	...	...	21	4	.	
R. triquetrus	...	...	...	10	14	16		
Sphagnum spp.	5	80	14	23	25	4		
Thuidium tamariscinum	10	...	...	3	...	...		

Barbilophozia floerkii	...	...	14	2	4	4
Lophozia ventricosa	...	...			7	4
Calypogeia trichomanis	...	...	14	5	7	...
Cephalozia bicuspidata	...	...	...	2	4	...
Cephaloziella sp.	5	20	14	2	...	...
Diplophyllum albicans	5	...	...	2	14	4
Lophocolea bidentata	19	60	43	10	21	12
Ptilidium ciliare	...	...	...	7	4	4
Scapania gracilis	5	...	...	2	4	...
Cladonia bellidiflora	10	...	...	2	...	4
C. coccifera	...	...	...	3	4	8
C. floerkeana	...	...	...	2	...	4
C. furcata	...	...	...	7	7	12
C. gracilis	10	...	14	16	14	20
C. impexa	5	...	...	2	...	4
C. pyxidata (incl. *C. chlorophaea*)	29	20	43	24	7	24
C. rangiferina	...	...	...	2	...	32
C. squamosa	10	...	29	11	4	16
C. sylvatica	19	20	57	34	14	44
C. uncialis	...	...	...	8	4	...
Peltigera sp.	...	...	...	5	7	12

Additional species recorded in one only of the community-types included in the table:

Lycopodium clavatum	5			*Betula pubescens*	3	*Polypodium vulgare*	7	*Betula* sp.	16	*Salix r*
Carex nigra	5			*Pinus sylvestris*	2	*Dactylorchis purpurella*	4	*Anemone nemorosa*	8	*Holcus*
Campylopus atrovirens	5			*Rubus fruticosus* agg.	2	*Juncus articulatus*	4	*Cirsium vulgare*	4	*Carex*
				Festuca vivipara	2	*Brachythecium rutabulum*	4	*Gnaphalium sylvaticum*	4	*C. flacc*
				Dactylorchis maculata ssp. *ericetorum*	3	*Aneura multifida*	4	*Hypochoeris radicata*	4	*Cerastii*
				Narthecium ossifragum	2	*Lepidozia setacea*	4	*Orthilia secunda*	4	*Galium*
				Alchemilla alpina	2	*Leptoscyphus taylori*	4	*Solidago virgaurea*	4	*Plantag*
				Melampyrum pratense	7	*Scapania umbrosa*	4	*Polytrichum alpestre*	8	*Prunell*
				Oxalis acetosella	2			*Barbilophozia barbata*	4	*Dicran*
				Teucrium scorodonia	2			*Tritomaria quinquedentata*	4	*Rhacom*
				Dicranella heteromalla	2			*Cladonia fimbriata*	4	*Tortula*
				Leptodontium flexifolium	2			*C. tenuis*	4	*Barbilo*
				Polytrichum formosum	2					*Frullan*
				Ptilium crista-castrensis	3					*Cetrari*
				Plagiochila sp.	2					*Platysm*
				Cladonia crispata	2					*Usnea*
				C. glauca	2					

Data from McVean and Ratcliffe (1962) have been incorporated in the above table.